The associations of the plant-ant *Cladomyrma* with plants in Southeast Asia

Dissertation
zur Erlangung des Doktorgrades
der Naturwissenschaften

vorgelegt beim
Fachbereich Biowissenschaften
der Johann Wolfgang Goethe-Universität
Frankfurt am Main

von
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aus Frankfurt am Main

Frankfurt am Main 2009

Vom Fachbereich .....
der J. W. Goethe-Universität, Frankfurt am Main, als Dissertation angenommen.

Dekan: .....

Gutachter: .....

Datum der Disputation: .....

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1. Preface

Ada gula ada semut
Malayan proverb

No plant can live in tropical regions without having personal contact with ants. What happens when these two worlds come together? What follows is a treatise on a rather extraordinary ant/plant complex. Specifically, this dissertation is about *Cladomyrma* plant-ants and their extremely extensive host plant range. In a broad sweep this study examines several aspects of the behavioural ecology of *Cladomyrma*, for example colony founding, host plant selection, acquisition of trophobiotic mealybugs, protection of their hosts against herbivorous insects, and effects of catastrophic events, such as flooding of nest chambers. Another major part of this study explores *Cladomyrma* taxonomy and host plant range in order to evaluate the degree of host specificity.

All these aspects touch some fundamental biological questions concerning mechanism of maintenance of diversity, e.g. habitat and/or host selection, intra- and interspecific competition and stochastic versus deterministic colonisation. Other major subjects in biology that are touched by this study are plant anti-herbivore defence systems and the evolution of interspecific mutualisms. Such mutualisms are widespread, but how they evolve is not clear. What factors promote the intimate interaction between unrelated organisms? Do these ant/plant associations show the potential for reciprocal evolutionary change, i.e., for coevolution?

Naturally, these subjects, being of major importance to biological science, cannot be treated here in depth. On the contrary, it is my intent to maintain a broad but rather superficial course by highlighting various different aspects, thus providing a first glance from different angles on this newly discovered ant/plant complex. The result is a puzzle with widely separated pieces and many gaps. Still, I hope that a picture emerges that serves as the framework for promising future research.

Let me say a few words regarding the so-called 'big science'. We presently live in a time when molecular biology and other types of big science receive far more attention by grant giving institutions than 'simple' field research. This trend will continue to reduce interest in whole-organism biology and natural history in both universities and the students they produce. But, as DEVRIES, CHACON & MURRAY (1992, p.123) have stressed earlier, "without data from the real world, no matter how sophisticated laboratory techniques or models become, in the absence of natural history they are unlikely to broaden our understanding of the myriad interactions among organisms." In my opinion, future insights into tropical biodiversity in general, and ant-plant mutualism specifically will demand a great deal more field work. The study on *Cladomyrma*/plant associations presented here illustrates this need.

The tropical rain forests display a biodiversity unparalleled by that of any other vegetation type. However, over the past few years I experienced a dramatic loss of tropical rainforest in some of my study areas. On the island of Borneo, for example, the natural forest cover is disappearing at a fast rate. Sabah, a federal state of Malaysia on Borneo, has almost depleted its primary forests outside conservation areas (UEBELHÖR & VON DER HEYDE 1993, RAMAKERS 1999, CHUNG et al. 2000, FITZHERBERT et al. 2008). Today, more than two thirds of the commercial forest reserves have been turned into second growth forests.

Secondary growth and selective logging, in turn, greatly enhance fire danger and, indeed, in the last two decades, fire has become one of the greatest threats to Bornean tropical rainforests (SIEGERT & HOFFMANN 2000). For the Bornean province East Kalimantan (Indonesia) alone it is estimated that during a severe drought caused by the 1997/98 El Niño phenomena, some 3 million hectare of forest (700,000 ha of protected forests and 2.3 million ha of natural forest concession areas), about 15% of the entire province, were affected by fire (HOFFMANN, HINRICHS & SIEGERT 1999). As yet there is no clear trend of a return to pre-disturbance conditions, which indicates that the burned forest may remain in a severely degraded state for a prolonged period of time (CLEARY & PRIDJATI 2005).

Certainly, several of the studied ant/plant associations will be strongly affected by these intense logging activities and increased fire danger. Although a few ant associations with pioneer host plant species seem to benefit - at least on a short-term basis - by these activities, I fear that in the long run they will be diminished as well. My observations suggest that the association with *Cladomyrma* is lost - even in pioneer hosts - when the distance to rainforest sources increases. A recent study by TANAKA et al. (2007) corroborates my assumption that deforestation can drastically decrease the

diversity of species involved in mutualistic interactions between ants and plants. Of course, it is not the ant/plant mutualisms alone which suffer from overexploiting logging. Recent calculations of extinction rates suggest that in tropical rain forests the absolute rate of species loss is now on the order of 1000 to 10,000 times higher than it was before human intervention (WILSON 1992, MCCANN 2000).

I am not in the position to criticise the politics of foreign countries such as Malaysia that certainly have the right to develop their resources. It is important to remember that the industrial nations also have very poor environmental records. However, forest resources in the tropics are too often controlled by a few powerful individuals that seem to regard logging as a prime opportunity for personal enrichment.

Why is biodiversity important to mankind? Would not the conservation of a few representative species of each genus or a higher taxon suffice? My answer is, in the words of PETER S. ASHTON (1996): "The problem is that biodiversity represents knowledge, like a major library: we never know which books we will need next, nor do we know which will yield the most information." I wish to add that biodiversity not only represents knowledge, it also arouses one of the most important human feelings – the impression of *beauty*. Those, who believe that such an argument is irrelevant or sentimental, are to be pitied.

Recent advances in biodiversity research suggest that diversity can be expected, on average, to give rise to ecosystem stability (TILMAN 2000). But so long as we are only beginning to understand how important species diversity is for the long term stability and function of ecosystems, our ethical imperative should be, if for no other reason, *prudence*. As EDWARD O. WILSON (1992, p. 335) says: "We should judge every scrap of biodiversity as priceless while we learn to use it and come to understand what it means to humanity. We should not knowingly allow any species or race to go extinct." Most people do not realise that we now cause one of the greatest extinction spasm of geological time. The diversity of life continues to diminish at an extremely fast rate, and in the bargain we shall erode the quality of our own life.

It is a faint hope that studies on tropical life - such as this dissertation - help to generate more respect for the rainforests with its wonderful creatures and interactions.

2. Notes on terminology

Several terms used in the present study must be defined at the outset so as to avoid misinterpretation. The terms *colonisation*, *inhabitation* and *occupation* are generally used here to signify that ants nest on the plant, i.e., that foundresses, queens, or workers with brood have been found. The two terms *myrmecophyte* and *domatium* are of considerable relevance to this study and therefore I will discuss the use of these terms in some depth.

2.1. Myrmecophyte

BELT (1874) was one of the first naturalists who formulated a coherent theory of *myrmecophily*, which was elaborated by DELPINO (1886). The BELT-DELPINO hypothesis stated that plants attract ants by supplying food and/or suitable lodgings for the ants and, in return, the ants defend the plants against their enemies. Others, such as SCHIMPER (1888), SCHUMANN (1888) and WASMANN (1889) joined BELT in asserting that these associations were mutualistic.

WARBURG (1892) proposed to replace the term *myrmecophilous* (ant-loving) plants by the term *myrmecophytes* (ant-plants), because the first implies that the plants have, in a sense, a biological interest in being visited by ants. In his definition *myrmecophyte* is a more neutral term, denoting plants that form some sort of a steady and regular relationship with ants. WARBURG (l.c.) further classified the *myrmecophytes* into plants offering food (myrmecotrophic) or lodging (myrmecodomic) or both (myrmecoxenic). Today, the term *myrmecophyte* includes WARBURG'S myrmecodomic and myrmecoxenic plants, whereas the myrmecotrophic plants are called *myrmecophiles*.

Ant-plants, or *myrmecophytes*, are thus briefly defined as plants which, during major parts of their life, are continuously inhabited by ants. This practical though incomplete definition, however, remained burdened with current philosophical theories on the presence or absence of symbiosis. The advocates of symbiosis were strongly criticised by an opposing party (e.g., RETTIG 1904, WHEELER 1910a, 1942, ESCHERICH 1911, BAILEY 1922a, 1923, SKWARRA 1935) who argued that the associations are fortuitous or exploitative, and IHERING (1907, paraphrasing R. SPRUCE 1873, cited in WALLACE 1905, p. 65) concluded that "*myrmecophytes have no more need of their ants than dogs have of their fleas*". At that time, ecological experiments with falsifiable predictions were not commonplace and the interpretation of the often detailed field observations was strongly influenced by the existing paradigm (FONSECA 1994).

Although evidence for beneficial ant-plant associations is now accumulating, the existing evidence to assess fitness consequences of particular associations is still often too meagre. In addition, recent studies have shown that some ant partners effectively reduce herbivory, but nevertheless are (temporarily) parasites that castrate their host (YU & PIERCE 1998, MOOG 2002, IZZO & VASCONCELOS 2002, GAUME, ZACHARIAS & BORGES 2002, MERBACH et al. 2007). In order to avoid placing the term *myrmecophyte* in dependency of an unknown *outcome* of the ant-plant association, the term is used here sensu DAVIDSON & MCKEY (1993a, p. 14), i.e., it only describes plants regularly inhabited by ants, without implying that host plants actually benefit from the ant tenants. Another definition of the term *myrmecophyte* is based on a morphological trait, i.e., it describes plant species that have evolved specialised structures (domatia) that house ants (BEQUAERT 1922). However, the term is used here (sensu LONGINO & HANSON 1995) also for plants that, in the absence of known *specialised* structures, are nevertheless regularly inhabited by one or more *plant-ant* species.[1] Even these two definitions cannot cover all the associations we find between plants and inhabiting ants since a continuum of specialisation towards myrmecophytism exists (for a review see BEATTIE 1985; JOLIVET 1996).

Another difficulty of the definition *myrmecophyte* lies in the condition of *regular* ant-inhabitation. Generally, ant occupancy rates of south-east Asian ant-plants are, with exception of myrmecophytic *Macaranga*, poorly studied. In the literature we find ant colonisation of particular plants often vaguely expressed as *usually*, *frequently*, *often* or *sometimes*. These terms are prone to misinterpretation. It may either just state occasional colonisations by opportunistic ants or is a reflection of the temporal and spatial variation of ant occupancy found in several ant-associated plants, e.g., colonisation frequencies depend on the developmental stage of the plant (FIALA & MASCHWITZ 1992a; GAY 1993b; MOOG, DRUDE & MASCHWITZ 1998) or is influenced by habitat and/or by proximity to foundress sources (YU & DAVIDSON 1997).

[1] Plant-ants are not just ants inhabiting ant-plants; this would be a circular argument. Traits of plant-ants include (i) colony foundation by ant queens in a particular host plant, (ii) a more or less strongly developed host specificity, (iii) host fidelity, defined here as the tendency of the ant colony to stay on the plant throughout the life of the colony, (iv) high occupancy rate, and (v) intraspecific competition for host plants.

2.2. Domatium

The Greek word *domatium* means *bedroom* or, according to the author of the word *domatium* as a biological term (LUNDSTROEM 1887), is a diminutive of the Greek word for *house* (little house). Since JACOBS' (1966) article "On domatia - the viewpoints and some facts," botanists mostly restrict the use of the term *domatia* to "spatial differentiations at the under surface of leaves, bound to nerves, and virtually always in or near their axils. They consist of a pit, a pocket, a hair-tuft, or a dome with an opening at its top, and these elements singly or variously combined." In other words, botanists condensed the definition of *domatia* to *acarodomatia* (mite shelter), the latter being practically interchangeable with *domatia*.

This is, however, not consistent with the original definition introduced by LUNDSTROEM (1887), who proposed a broader concept of the term: "Unter *Domatien* verstehe ich alle besonderen Bildungen an einem Pflanzentheile oder Umwandlungen eines solchen, welche für andere Organismen bestimmt sind, die als mutualistische Symbionten - d.i. solche Organismen, die zu den Wirthen, welche sie bewohnen, in einem Verhältniss gegenseitiger Förderung stehen - einen wesentlicheren Theil ihrer Entwicklung daselbst durchmachen." In LUNDSTROEM'S definition the term *domatia* describes all such features found in a plant that are intended to harbour mutualistic symbionts during an essential part of the development of these symbionts. Basically, I will follow LUNDSTROEM'S definition by using the term *domatia* in the sense of *myrmecodomatia* (ant-houses). Nevertheless, his definition suffers from the vaguely expressed condition of "features *intended* to harbour mutualists." This study will show that the degree of specialisation of a certain structure to house ants is often unclear. The apparent continuum of specialisation in hosts of *Cladomyrma* ants will be treated in more detail in chapter 4 (4.4.5.).

LUNDSTROEM has also been criticised for including in his definition the assumption of a beneficial relationship between the domatia inhabitants and the host plant (JACOBS 1966). As JACOBS (p. 314) put it: "A biological relationship between domatia-bearing plants and Acari has never been proved; the idea can be traced to suppositions concerning myrmecophily, which are obsolete since a long time." During the last decades, however, it became clear that the impact of indirect plant defences, mediated by mites or ants, has been largely underrated (for mites: e.g., AGRARWAL & KARBAN 1997, O'DOWD & PEMBERTON 1998, SABELIS et al. 1999, AGRARWAL, KARBAN & COLFER 2000, NORTON, ENGLISH-LOEB & BELDEN 2001, and for ants: e.g., JANZEN 1966, 1967 and 1969a, RISCH et al. 1977, MCKEY 1984, FIALA et al. 1989, FONSECA 1994, ALONSO 1998, FEDERLE, MASCHWITZ & FIALA 1998b, GAUME & MCKEY 1998, MOOG, DRUDE & MASCHWITZ 1998, STAPLEY 1998, BIZERRIL & VIEIRA 2002).

3. Revision of the genus *Cladomyrma* [2]

3.1. INTRODUCTION

The importance of biodiversity lies not simply in numbers but in how organisms live and interact within habitats. Thus an important aspect of the study of ant-plant mutualisms concerns identification of ant symbionts. A basic knowledge of the taxonomy of the mutualistic partners is a necessity for a well-founded interpretation of the ecology and evolutionary biology of ant-plant interactions. However, studies on such systems face the problem of complex patterns of species associations. Whereas the number of involved ant-plant species in such mutualisms is comparatively easily assessed, the diversity of plant-ants is often subject to speculation. This is true for the *Cladomyrma*-plant associations as well. Since the last revision of this genus (AGOSTI 1991), more material has become available. During the last decade, many more host plants of *Cladomyrma* have been found. According to current knowledge, *Cladomyrma* inhabits live stems of 24 species of host plants in ten different genera, thus colonising about 50% of all non-epiphytic plant genera, which are known to be regularly associated with specialised stem-nesting ant partners in the Oriental region (MOOG et al. 2003, this thesis). The ant partners of the recently found host plants not only belong to specific species but to hitherto undescribed species as well, thus illustrating the need for a renewed basic taxonomic treatment.

As most of the genera of formicine ants are characterised by the absence of discrete characters and an extensive variation in characters such as shape or position and number of hairs, large series are needed to extract species-specific characters. Changes in the status of species might thus occur, and are well illustrated in this study. Nevertheless, I consider the acceptance of status changes better than the use of informal names not accompanied by diagnoses. In addition, the positive identification of species in some ant groups is difficult or impossible without specimens of the reproductive castes. This is true for the formicine genus *Cladomyrma* as well. The best characters to separate species in *Cladomyrma* are in the male and the queen caste. Whereas few males are known to date, queens are often abundant in this material. Based on the variation of queens, more species can be diagnosed than with workers alone. This, in turn, often makes it impossible to identify workers without

[2] The revision has been written in cooperation with Donat Agosti, Dep. of Entomology, American Museum of Natural History (see AGOSTI, MOOG & MASCHWITZ 1999). In the version presented here, the status of species is maintained, however, additional information on newly collected *Cladomyrma* populations are given and new distribution maps are provided.

their queen. This revision aims at reassessing the status of the previously described species, describing the new species, and presenting a key to the queen caste.

3.2. MATERIAL AND METHODS

Measurements were taken at 50 x magnification under a binocular microscope. Repeated test measurements produced an error of *c*. ± 0.005 mm. All measurements are given as minimum and maximum; the unit is mm; e.g., AL 1.23–1.45. Morphological terminology follows BOLTON (1994).

Alitrunk length (AL)	The diagonal length of the alitrunk (= mesosoma) in profile from the anteriormost point of the pronotum to the posteriormost point of the metapleuron
Eye length (EL)	The maximum diameter of the eye
Head length (HL)	The length of the head proper, excluding the mandibles, measured from the mid-point of the anterior clypeal margin to the mid-point of the occipital margin, in full-face view
Head width (HW)	The maximum width of the head in full-face view, measured below the eyes
Scape length (SL)	The maximum straight line of the antennal scape excluding the basal constriction or neck of the condylar bulb
Cephalic index (CI)	HW x 100 / HL
Eye index (EI)	EL x 100 / HW
Scape index (SI)	SL x 100 / HW

Colour images of workers are available at:

www.eol.org
www.antweb.org
www.antbase.net

Collections

Most of the material examined comes from the author's and U. MASCHWITZ's collections in Southeast Asia and is deposited at several institutes (see below). DIANE DAVIDSON and BRIGITTE FIALA provided additional new material. We are grateful to BARRY BOLTON (NHM), STEFAN COVER (MCZ), VALTER RAINERI (MCSN), and ROY SNELLING (LACM) for their help in the loan of specimens.

Institutional abbreviations

AMNH American Museum of Natural History, New York, USA
FRIM Forest Research Institute of Malaysia, Kepong, Malaysia
LACM Los Angeles County Museum, Los Angeles, USA
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, USA
MSNG Museo Civico di Storia Naturale, Genoa, Italy
NHM The Natural History Museum, London, UK

Collectors

DD Diane Davidson
BF Brigitte Fiala
JM Joachim Moog
UM Ulrich Maschwitz

3.3. RESULTS AND DISCUSSION

***CLADOMYRMA* Wheeler**

Cladomyrma Wheeler 1920: 53. Type species *Aphomomyrmex hewitti* Wheeler, 1910: 132, by original designation.

Taxonomic history

A single *Cladomyrma* queen from Borneo was first described as *Dimorphomyrmex andrei* (EMERY 1894: 73) and later included in *Aphomomyrmex* by the same author after he had seen African *A. afer* (EMERY 1899: 494). WHEELER (1910b: 132) listed both species and described a third, *A. hewitti*, based on two queens and eight workers collected in Borneo. In 1920 WHEELER (p. 53) placed the two Bornean members of *Aphomomyrmex* into a new genus, *Cladomyrma*, with *A. hewitti* as genotype. DONISTHORPE (1937: 620) described a third species, *C. hobbyi*, from three winged queens taken in Borneo. The first revision of the genus, based on new material from Malay Peninsula and Borneo, recognised five species (AGOSTI 1991). A brief summary of the taxonomic history is listed in Tab. 3-1.

Phylogenetic relationship

The old world genera *Aphomomyrmex*, *Cladomyrma*, and *Petalomyrmex* and the new world genus *Myrmelachista* are all, except for some in *Myrmelachista*, obligatory inhabitants of internodes of rainforest trees and vines. Living in hollow branches and caulinary domatia of climbers and trees, which are actively opened by the queen, their

lifestyle is a possible synapomorphy for these genera. All the queens of these plant-ant genera show a ± flattened head and alitrunk, which has been interpreted as an adaptation to their life in plant cavities (MCKEY 1991). Therefore, the question has been raised as to whether they form a monophyletic taxon (MASCHWITZ et al. 1991, CHENUIL & MCKEY 1996). However, the phylogenetic relationship of *Cladomyrma* within the Formicinae is unclear (see Tab. 3-1).

Table 3-1: Taxonomic history of *Cladomyrma* (presently accepted names in **bold**).

Taxon	Tribe	Reference
Dimorphomyrmex andrei		EMERY 1894
Aphomomyrmex andrei		EMERY 1899
A. hewitti		WHEELER 1910b
Cladomyrma andrei, ***C. hewitti***	Myrmelachistini	WHEELER 1920
	Dimorphomyrmicini	EMERY 1925
C. hobbyi	Dimorphomyrmicini	DONISTHORPE 1937
	Brachymyrmecini	WHEELER & WHEELER 1976, 1985
	Myrmelachistini	HÖLLDOBLER & WILSON 1990
C. cryptata, ***C. maschwitzi***, *C. mossyna*, ***C. petalae***	*Lasius* genus-group	AGOSTI 1991
	Brachymyrmecini	BOLTON 1994, 1995a
	Brachymyrmecini	BROWN 2000
	Lasiini	BOLTON 2003

Cladomyrma was described by WHEELER (1920) as a myrmelachistine genus, and he also included in the same tribe *Aphomomyrmex*, *Brachymyrmex*, and *Myrmelachista*. EMERY (1925) redefined Myrmelachistini to include only two genera *Myrmelachista* and *Stigmacros*, and he placed *Aphomomyrmex*, *Brachymyrmex*, *Cladomyrma*, *Dimorphomyrmex*, and *Gesomyrmex* in the tribe Dimorphomyrmicini. Based on a combination of larval characters WHEELER & WHEELER (1976, 1985) included African *Aphomomyrmex* and *Petalomyrmex*, Neotropical *Brachymyrmex*, and Asian *Cladomyrma* in Brachymyrmecini and Neotropical *Myrmelachista* in Myrmelachistini. This is not reflected in HÖLLDOBLER & WILSON's (1990) classification, which included *Aphomomyrmex*, *Brachymyrmex*, *Cladomyrma*, *Myrmelachista*, *Petalomyrmex*, and *Pseudaphomomyrmex* in the tribe Myrmelachistini and therefore did not exclude a possible monophyletic origin for those genera.

After examining one queen syntype of *Cladomyrma hewittii* and comparing it with *Petalomyrmex phylax* and *Aphomomyrmex afer*, SNELLING (1979) confirmed that

Cladomyrma and *Aphomomyrmex* represent distinct ant genera. SNELLING did not comment on possible relationships. A new classification of the Formicinae, based on new morphological characters at the generic level, was proposed by AGOSTI (1991), who placed *Cladomyrma* in the *Lasius* genus-group and *Aphomomyrmex*, *Myrmelachista*, and *Petalomyrmex* in the *Pseudolasius* genus-group, thus making the monophyly of the plant-ant genera *Aphomomyrmex*, *Cladomyrma*, *Myrmelachista* and *Petalomyrmex* unlikely. AGOSTI (1991) considered *Acropyga* as a possible sister group of *Cladomyrma* within the *Lasius* genus-group.

There have been since continued changes in the tribal classification of *Cladomyrma* (BOLTON 1994, 1995a, 2003; Brown 2000), and its phylogenetic relationship to other formicine genera containing plant-ants remained ambiguous. A recent morphological analysis, however, provides evidence that Asian *Cladomyrma* is most closely related to New World *Myrmelachista* and *Brachymyrmex* (LAPOLLA & LONGINO 2006). Examination of the male genitalia show that only these three genera possess an apodemal ridge running along the dorsal margin of the penis valve. This study also suggests that the African genera *Aphomomyrmex* and *Petalomyrmex* are no close relatives of *Cladomyrma*. Furthermore, molecular evidence from the D2 region of the 28S ribosomal RNA and EF1-alpha protein-coding genes place *Brachymyrmex* and *Cladomyrma* together (*Myrmelachista* was not included in the analysis) (LAPOLLA et al. 2006).

The lack of discrete characters makes it difficult to assess phylogenetic relationships within *Cladomyrma*. Two groups might be recognised by the shape of the queen petiole, which in one case is dorsally truncated and low, and in the other an erect node or scale. Whereas some species, such as *crypteroniae* and *maschwitzi*, are very distinct, most other species require some expertise or reference collections for identification.

Diagnosis

Cladomyrma is easily recognised among formicine ants by (i) the presence of a minor worker and soldier caste (major worker), (ii) an angulate outer margin of the mandible in the soldier caste (Fig. 3-4) and the queen (Fig. 3-3), (iii) eight antennal segments in queens and workers, and (iv) a well developed acidopore. A full diagnosis of the genus is provided in AGOSTI (1991).

Workers of *Cladomyrma* are strictly dimorphic, with majors and minors (COLON, MOOG & MCKEY, in preparation). The main diagnostic differences are:

- mandibles with seven to nine teeth in minor workers, four teeth in major workers
- in full frontal view, sides of head subparallel in majors, convex in minors
- in frontal view, the lateral portion of the clypeus (at the mandibular articulations) distinctly surpass the central front margin of the clypeus in majors (Fig. 3-4)
- minors usually have a uniform, dense pubescence, majors have sparse pubescence on the occiput (hairs shorter than their interspace)
- body of majors stouter, with bigger head size in relation to hind tibia length

Previous investigations on *Cladomyrma* ants have been limited. A structural analysis of the proventriculus ('gizzard') is given in EISNER (1957). PCR primers for polymorphic microsatellite loci, originally developed for the plant-ant *Petalomyrmex phylax*, were also tested in two *Cladomyrma* species (DALECKY et al. 2002). Two or three of the 14 primer pairs tested may successfully be used as a taxonomic tool in *Cladomyrma*.

Size

The size of workers is rather variable during a colony cycle, with the first workers (nanitics) being much smaller than those after the presence of some thirty workers or more. In addition, workers of large, mature colonies are still larger (and usually darker) than those of medium-sized colonies. Worker size alone is therefore a very ambiguous character for the identification of species.

Distribution

Cladomyrma has been thought to be restricted to the ever-wet part of the West Malesian floristic region, comprising the Malay Peninsula, Borneo, and Sumatra (Fig. 3-1). However, the genus was recently collected from tropical seasonal forests at the Cuc Phuong NP, North Vietnam (YAMANE et al. 2002) and Nam Tok Phliu NP, Eastern Thailand (FUJIWARA et al. 2004). The specimens collected in Vietnam have been described as a new species, *C. scopulosa*, by EGUCHI & BUI (2006). *Cladomyrma* is not known east of the Makasar Strait, in Sulawesi. Another clearly defined boundary appears to be the Sunda Strait; no records exist from Java. The majority of species are known to occur in Borneo and Peninsular Malaysia. A field trip first recorded *Cladomyrma* with two species, *maschwitzi* and *crypteroniae*, in Sumatra. A previous record from Sumatra (ROEPKE 1930) is a misidentification of an *Acropyga* species (REYNE 1965). Field observations indicate that the uppermost altitudinal limit of the vertical distribution of *Cladomyrma* is about 1,300–1,350 m; thus its natural habitats comprise of lowland, hill and upper dipterocarp forests. An account of the species distribution is given at the end of this chapter (Fig. 3-9).

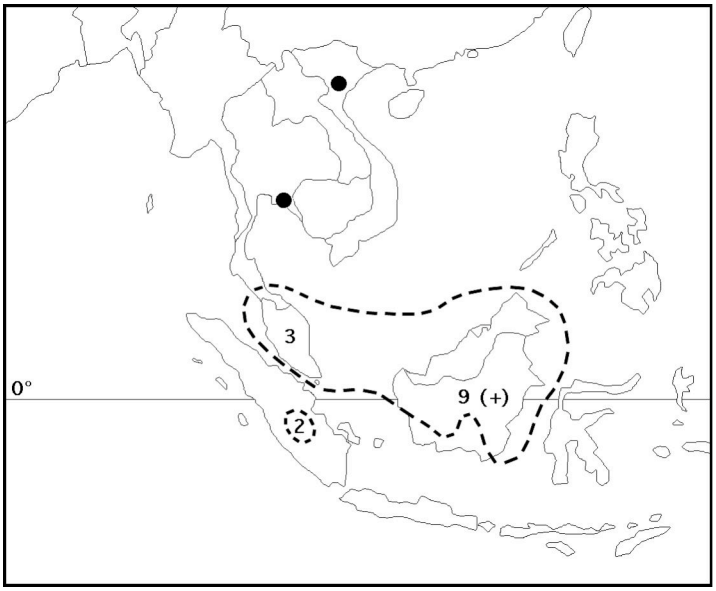


Figure 3-1: Distribution of *Cladomyrma* plant-ants in SE Asia according to field and herbarium data (*broken line*). The number of known *Cladomyrma* species is indicated for each geographic region. In Sumatra, *Cladomyrma* has been found only in a rather small region (part of Jambi and Sumatra Barat). Only recently, the genus has been recorded in Thailand and at the Cuc Phuong NP in North Vietnam (black dots). [Distribution maps for each species are provided below; see Fig. 3-9]

3.3.1. Synopsis of species (as in AGOSTI, MOOG & MASCHWITZ 1999)

Depressed petiole group:

andrei (Emery)
= *cryptata* Agosti **syn. nov.**
hobbyi Donisthorpe **stat. rev.**
maschwitzi Agosti
nudidorsalis Agosti, Moog & Maschwitz **sp. nov.**
petalae Agosti
= *mossyna* Agosti **syn. nov.**
yongi Agosti, Moog & Maschwitz **sp. nov.**

Raised petiole group:

aurochaetae Agosti, Moog & Maschwitz **sp. nov.**
crypteroniae Agosti, Moog & Maschwitz **sp. nov.**
dianeae Agosti, Moog & Maschwitz **sp. nov.**
maryatiae Agosti, Moog & Maschwitz **sp. nov.**
hewitti (Wheeler) **stat. rev.**

3.3.2. Key to the queen caste

1 Dorsum of mesonotum without erect hairs (Fig. 3-2D) ***nudidorsalis***
- Dorsum of mesonotum with erect hairs **2**

2 Whole body yellow **3**
- Body bicoloured or light to dark brown; if light brown, gaster darker than alitrunk, or tergites bicoloured **4**

3 Wide alitrunk; petiole raised, in lateral view dorsally truncated (Fig. 3-2I) ***crypteroniae***
- Narrow alitrunk; petiole in lateral view low and dorsally truncated (Fig. 3-2A) ***andrei*** (part)

4 Petiole in lateral view dorsally truncated, low, and dorsolaterally distinctly angulate **5**
- Petiole in lateral view forming an upright scale or node, dorsolaterally rounded **9**

5 Dorsal part of katepisternum shining and without pubescence (Fig. 3-6A) ***petalae***
- Dorsal part of katepisternum punctulate and with pubescence (Fig. 3-6B) **6**

6 Head and alitrunk bright yellowish brown with distinctly darker gaster; small (AL < 2.1 mm); larger metapleural gland orifice (Fig. 3-2E) ***yongi***
- Head and alitrunk brown to dark brown or reddish; size variable **7**

7 Whole body (light) brown (Fig. 3-2C) ***maschwitzi***
- Whole body dark brown or bicoloured, generally with dorsum of alitrunk reddish brown **8**

8 Dorsal part of katepisternum dull or at least covered with long pubescence; head short to somewhat elongate (Fig. 3-2A); larger ants (AL > 2.00 mm) ***andrei*** (part)
- Dorsal part of katepisternum punctulate, shining and with a sparse pubescence with thin hairs; roundish, elongate head with genae distinctly brightest coloured part of the head (Fig. 3-2B); generally smaller ants (AL < 2.20 mm) ***hobbyi***

9 Erect hairs only on dorsal parts of gastral tergites 2 and 3 along the posterior margin **10**
- Erect hairs scattered all over second gastral tergite **11**

10 None or very few short pubescent hairs on gastral tergite 2; long erect, curved hairs on gastral tergite 1; wide alitrunk; larger body (Fig. 3-2H) ***aurochaetae***
- Regularly, but very widely spaced pubescence on gastral tergite 2; erect hairs on gaster tergite 1 not very long and not regularly curved; narrower alitrunk; smaller (Fig. 3-2L) ***maryatiae***

11 Head longer, CI < 83, parallel sided in full frontal view (Fig. 3-2K); gastral tergites with long erect hair at the posterior margin of the tergites ***hewitti***
- Head shorter, CI > 82 or at least sides slightly rounded in frontal view (Fig. 3-2J); gastral tergite covered with long erect hair ***dianeae***

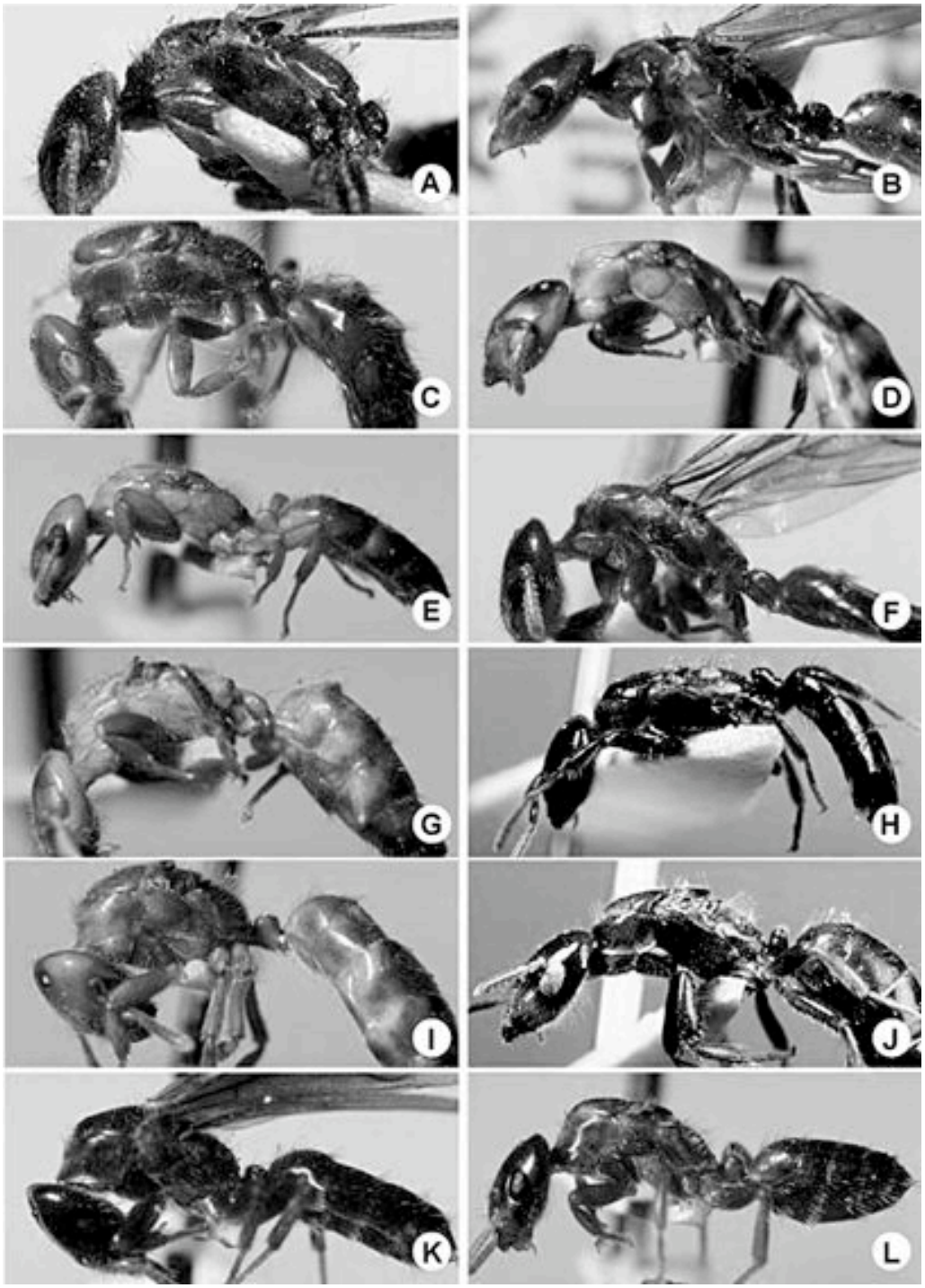


Figure 3-2: Lateral view of *Cladomyrma* queens. **A** *andrei* (dark form); **B** *hobbyi*; **C** *maschwitzi*; **D** *nudidorsalis*; **E** *yongi*; **F** *petalae*, dark form; **G** *petalae*, light form; **H** *aurochaetae*; **I** *crypteroniae*; **J** *dianeae*; **K** *hewitti*; **L** *maryatiae*. © Courtesy of Donat Agosti.

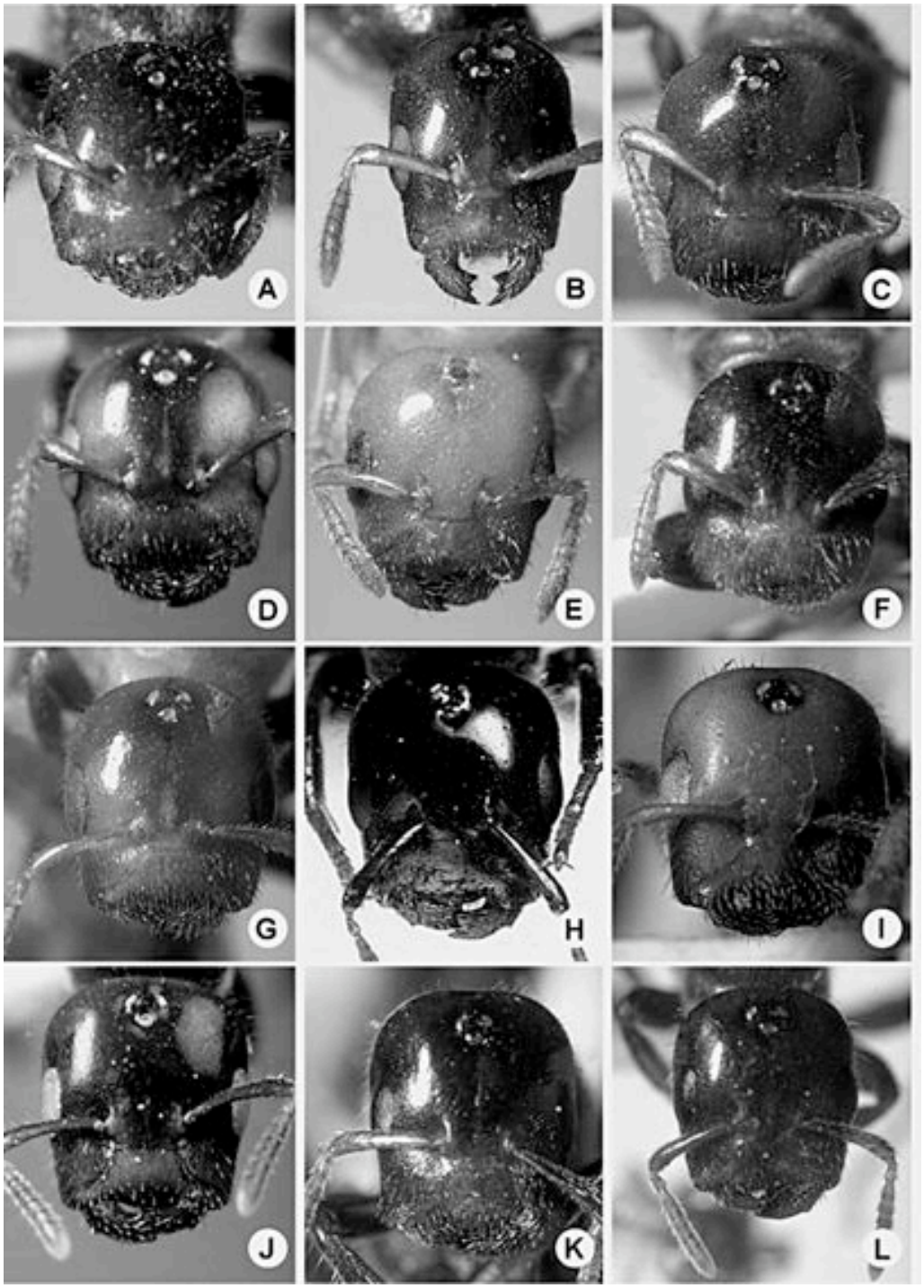


Figure 3-3: Head of *Cladomyrma* queens in full frontal view. **A** *andrei*; **B** *hobbyi*; **C** *maschwitzi*; **D** *nudidorsalis*; **E** *yongi*; **F** *petalae*, dark form; **G** *petalae*, light form; **H** *aurochaetae*; **I** *crypteroniae*; **J** *dianeae*; **K** *hewitti*; **L** *maryatiae*. © Courtesy of Donat Agosti.

3.3.3. Species accounts

Depressed Petiole Group

Cladomyrma andrei (Emery)

Figures 3-2A, 3-3A, 3-7(1)

Dimorphomyrmex andrei Emery, 1894:73. (Later combinations: *Aphomomyrmex andrei* Emery, 1899: 494; *Cladomyrma andrei*, Emery 1925: 45). Syntype queen, BORNEO: Indonesia, South Kalimantan, Poulo Laut, leg. W. Doherty; MCSN [examined].

Cladomyrma cryptata Agosti, 1991: 304. Holotype queen, BORNEO: East Malaysia, Sabah, Poring Hot Springs, #815, leg. UM, ex *Callerya* (= *Millettia*) *nieuwenhuisii*; BMNH. **Syn. nov.**

Diagnosis

Major worker: AL 0.84-1.64, HL 0.86-1.42, HW 0.76-1.32, EL 0.16-0.30, SL 0.38-0.68, CI 89-98, EI 21-42, SI 44-53 (n=8). Generally larger body size; pilosity and dorsum of alitrunk and gaster variable, generally short and not very dense; generally reddish dark brown to dark brown; clypeus angulate; gastral pubescence thin, hair at least as long as distance between their insertions. **Minor worker**: AL 0.64-1.00, HL 0.59-1.04, HW 0.52-0.78, EL 0.13-0.22, SL 0.29-0.46, CI 83-95, EI 23-27, SI 55-66 (n=8). Generally larger body size; pubescence on gaster dense, short and appressed; metapleural gland orifice large. **Queen**: AL 2.08-2.56, HL 1.30-1.46, HW 1.02-1.24, EL 0.47-0.54, SL 0.61-0.78, CI 76-86, EI 40-47, SI 58-66 (n=17). Large body size (AL > 2.0 mm); body colour usually dark brown to black (rarely uniformly yellowish); head distinctly bicoloured with genae and clypeus lighter than the remainder of the head capsule; metapleural gland orifice large but covered with a bunch of hairs inserted ventrally to the opening; petiole low and dorsally truncated; gaster with many long erect hairs scattered all over the tergites and generally appressed, widely set pubescence.

Paratype: Queen AL 2.28, HL 1.36, HW 1.14, SL 0.68, EL 0.53, CI 84, EI 46, SI 60

Comments

The species belongs to the larger Bornean species of *Cladomyrma*. It is the most variable species, with variation in size; head shape, from a very short to a medium long head; body colour, almost black to brown (rarely uniformly yellowish [one collection]); and gastral hairs, which can be long to short. The status of this species is similar to that of *petalae* (see below). Although there might be several species included, it is at the very moment impossible to separate them.

The typical *cryptata* (syn. nov.) and *andrei* differ somewhat in the fine chagrinate sculpture on the head and the mat surface, which is very distinct in *cryptata* as opposed to the brilliant shining and completely smooth surface in *andrei*. The type series of *cryptata* includes one queen with a short head and one with an elongate head, which is similar to the type of *andrei*. Another variation includes workers from Poring Hot Springs (JM #95-018 and #95-017) which have a slightly elongated head, and very conspicuous long, heterogeneous hairs (some longer than others) on the dorsum of the alitrunk. In contrast, the workers of the typical *andrei* have subhomogeneous setae not reaching the length of the former. This variation is also the only population of *andrei* living in *Drypetes longifolia* (Putranjivaceae, formerly part of Euphorbiaceae).

One collection (JM #93-061) shows a uniformly yellowish coloured queen, but it closely resembles *andrei* (*cryptata* form) in most characters except in body colour. A very slight difference in the density of the pubescence was observed on the anterior and lateral parts of the mesonotum, but since this character exhibits some variation in *andrei* it was not used to erect a new species. Considerable variation in body colour of queens may be a rather common phenomenon in *Cladomyrma* (see under *petalae*).

Biology and distribution

The species has been found colonising the endemic woody climbers *Callerya nieuwenhuisii* (MASCHWITZ et al. 1989), *Spatholobus oblongifolius* (both Papilionaceae), and the tree genus *Drypetes* (Putranjivaceae). In Poring Hot Springs, Sabah, samples of this species have been obtained on a canopy walkway from a huge *Callerya*, about 40 m above ground. It is supposed that *andrei* is distributed over all of Borneo since the type specimen was collected in South Kalimantan (Poulo Laut). Most records are, however, from Sabah and Sarawak, whereas Kalimantan is poorly sampled (Fig. 3-9).

Material examined

Type: INDONESIA, South Kalimantan, Poulo Laut, Doherty, MCSN, queen. **Other specimens**: EAST MALAYSIA, Sabah, Ranau, Poring Hot Springs, 14.xi.1992, Leg. BF, #0052, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Sabah, Ranau, Poring Hot Springs, 22.i.1989, leg. UM, #0815, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Sabah, Ranau, Poring Hot Springs, 28.i.1993, leg. JM, #93-061, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*, alt.: ca. 600 m, colony size: 11 workers in total; Sabah, Ranau, Poring Hot Springs, 26.i.1995, leg. JM, #95-017, ex: *Drypetes longifolia*, young colony: ca. 200 workers in total, alt.: ca. 800 m; Sabah, Ranau, Poring Hot Springs, 26.i.1995, 95-018, leg. JM, ex: *Drypetes longifolia*, mature colony, alt.: ca. 800 m; Sabah, Ranau Poring

Hot Springs, 02.v.1987, leg. Burckhardt & Löbl; Sarawak, Lambir NP, Miri, 25.ii.1992, leg. UM, #92-222, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 25.ii.1992, leg. UM, #92-224, 92-224a and 92-224c, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Sarawak, Lambir NP, Miri, 25.ii.1992, leg. UM, #92-227, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Sarawak, Lambir NP, Miri, 17.ii.1995, leg. JM, #95-060, ex: *Spatholobus oblongifolius*, mature colony. INDONESIA, Kalimantan, 14.xi.1992, leg. BF, #0126, ex: *Callerya* (= *Millettia*) *nieuwenhuisii*; Kalimantan, Balikpapan, 16.xi.1992, leg. BF, #0182, ex: *Spatholobus oblongifolius*.

Cladomyrma hobbyi Donisthorpe stat.rev. [revision of 1999]

Figures 3-2B, 3-3B, 3-4A

Cladomyrma hobbyi Donisthorpe, 1937: 620. Holotype queen, BORNEO: East Malaysia, Sarawak, Mt. Dulit, 4500 ft, moss forest, 14.x.1932, leg. B. M. Hobby; BMNH [examined; synonym of *C. andrei*, Agosti 1991: 303]. Stat. rev.

Diagnosis

Major worker: AL 0.80-1.08, HL 0.94-1.02, HW 0.64-0.90, EL 0.14-0.18, SL 0.32-0.46, CI 82-89, EI 18-23, SI 50-53 (n=8). Frons without longitudinal, brighter coloured spot; clypeus truncated (= angulate in lateral view); short, square head; small body size; gastral pubescence relatively widely set, but hair longer than the distance between their insertions. **Minor worker**: AL 0.57-0.82, HL 0.59-0.70, HW 0.48-0.64, EL 0.10-0.14, SL 0.28-0.36, CI 83-91, EI 21-29, SI 53-61 (n=8). Small body size; body yellowish brown, with genae slightly more yellowish; metapleural gland orifice large; gastral pubescence relatively widely set, but hair longer than the distance between their insertions. **Queen**: AL 1.84-2.16, HL 1.18-1.28, HW 0.93-1.00, EL 0.40, SL 0.54-0.62, CI 75-80, EI 43-47, SI 57-63 (n=8). Head elongate, clypeus smoothly rounded in lateral view; dorsal part of katepisternum with widely set, extremely thin and thus hardly visible pubescence; shining; low petiole, posteriorly gently declining; dense pubescence on gastral tergites; erect hairs scattered all over the tergites; dorsum of alitrunk brownish red coloured, distinct from head and gaster. **Male**: Petiole a high node; subgenital plate long, slender, parallel-sided and apically truncated; stipites apically wide, extended and almost hemispherical; small body size.

Paratype: Queen: AL 2.16, HL 1.28, HW 0.99, SL 0.62, EL 0.46, CI 77, EI 46, SI 63

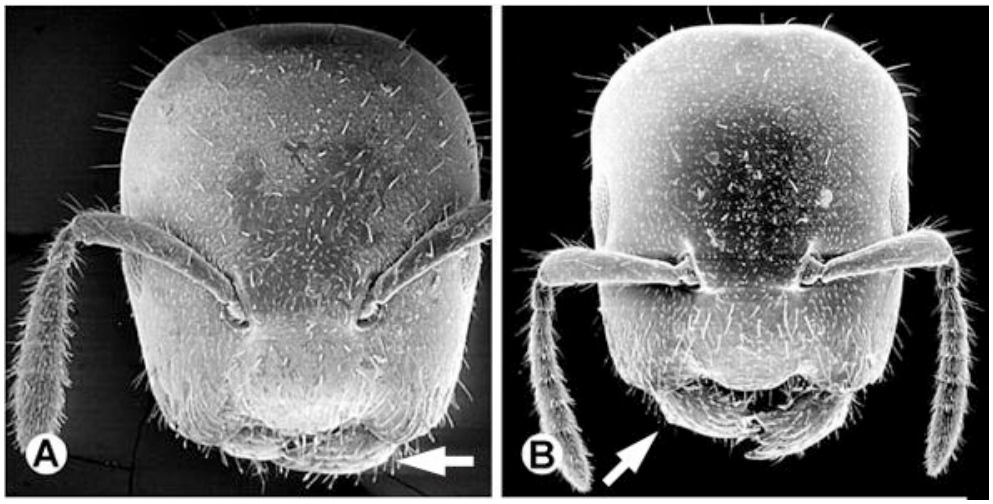


Figure 3-4: Head in full frontal view of major worker (SEM); **A** *hobbyi*; **B** *maryatiae*. Arrows indicate the angulate outer margin of the mandible.

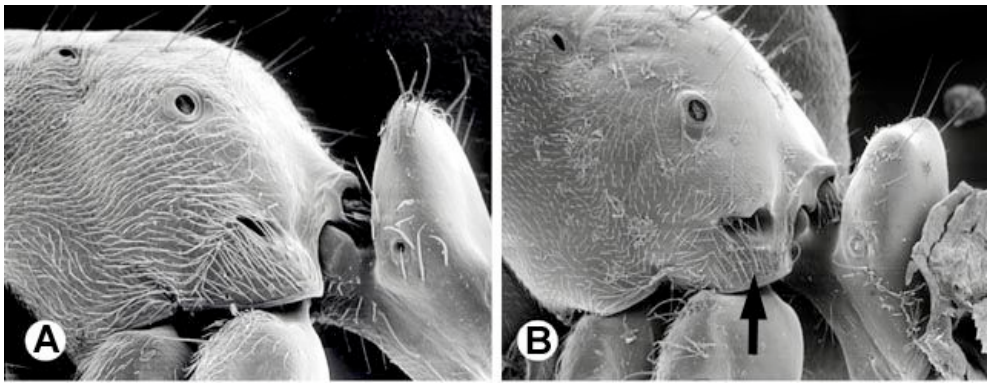


Figure 3-5: Metapleural gland orifice of workers (SEM); **A** *petalae*; **B** *dianeae*. Note the long erect setae that cover the metapleural gland orifice (arrow).

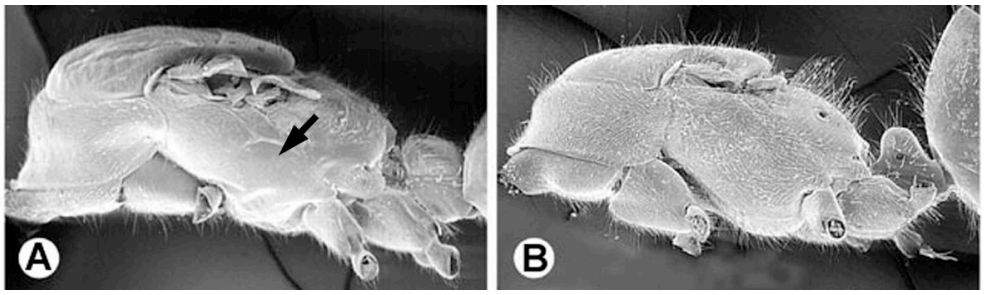


Figure 3-6: Alitrunk and petiole of queens in lateral view (SEM); **A** *petalae*; **B** *maryatiae*. Note the shining dorsal part of the katepisternum (arrow) in *petalae*, and the difference in petiole shape, 'depressed' in *petalae* versus 'raised' in *maryatiae*.

Comments

All the series available have extremely small workers. The gently rounded dorso-posterior corner of the petiole of the queens is typical for this species, separating it especially from queens of *andrei*, which, in addition, have a rather bright coloured and elongate head.

Biology and distribution

This species has been collected from the woody climber *Spatholobus oblongifolius* (Papilionaceae) and the understorey tree *Drypetes longifolia* (Putranjivaceae) in Lambir NP, Miri, Sarawak (Fig. 3-9). The type specimens have been obtained by light traps on Mt. Dulit at an altitude of ca. 4,500 ft (= ca. 1,350 m). I assume that the host plant source was a *Spatholobus*. Whereas *Drypetes* does not occur above 900 m (pers. observation) the liana, according to herbaria notes, extends at least up to 1,000 m and, furthermore, is known from that locality. I found the Malayan counterpart, *Spatholobus bracteolatus*, at an elevation of 1,300 m, by far exceeding the altitudinal range mentioned on herbarium labels. Therefore, it may be possible that the type specimens originate from *S. oblongifolius*.

Material examined

Syntype (labeled "Cotype"): EAST MALAYSIA, Sarawak, foot of Mt. Dulit, junction of rivers Tinjar and Lejok, 01.ix.1932, leg. B.M. Hobby and A.W. Moore, B.M. 1933-524, queen, ex: light trap, MCZ. **Other specimens**: EAST MALAYSIA, Sarawak, Lambir NP, Miri, 25.ii.1992, leg. UM, #92-218, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 25.ii.1992, leg. UM, #92-221 b, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 27.ii.1992, leg. UM, #92-233, ex: *Drypetes longifolia*; Sarawak, Lambir NP, Miri, 17.ii.1995, leg. JM, #95-061, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 17.ii.1995, leg. JM, #95-064, ex: *Spatholobus oblongifolius*; Sarawak, Lambir NP, Miri, 18.ii.1995, leg. JM, #95-065, ex: *Spatholobus oblongifolius*, young colony: 150 workers in total; Sarawak, Lambir NP, Miri, 22.ii.1995, leg. JM, #95-078, ex: *Drypetes longifolia*, colony size small (worker = nanitics), despite presence of males! Whole plant dissected; Sarawak, G. Mulu NP, ?.ii.1978, leg. JH; G. Mulu, light trap; Sarawak, Mt. Dulit, leg. F. Mjoeberg, MCZ; Sarawak, Lambir NP, Miri, 27.ii.1992, leg. UM, #92-235, ex: *Drypetes longifolia*.

Cladomyrma maschwitzi Agosti

Figures 3-2C, 3-3C, 3-7(2)

Cladomyrma maschwitzi Agosti, 1991: 306. Holotype queen, WEST MALAYSIA, Selangor, Ulu Gombak, 1990, #3, ex *Crypteronia griffithii*, leg. JM; BMNH.

Diagnosis

Major worker: AL 0.84-1.00, HL 0.81-0.98, HW 0.68-0.82, EL 0.15-0.20, SL 0.38-0.48, CI 83-85, EI 22-25, SI 53-59 (n=8). Median part of clypeus coarsely sculptured; large, open metapleural gland orifice; whole body light yellow coloured; few hairs on the dorsum of the mesonotum. **Minor worker**: AL 0.68-0.71, HL 0.62-0.65, HW 0.52-0.56, EL 0.12-0.14, SL 0.32-0.34, CI 84-87, EI 22-25, SI 57-63 (n=8). Large, open metapleural gland orifice; whole body light yellow coloured. **Queen**: AL 1.82-2.38, HL 1.22-1.41, HW 0.98-1.06, EL 0.44-0.48, SL 0.62-0.68, CI 74-80, EI 44-49, SI 63-66 (n=6). Whole body (light) brown. Dense, subdecumbent pubescence on scape, occiput and alitrunk; an- and katepisternum with few erect hairs, especially in the dorsal regions; large metapleural gland orifice; petiole low, dorsally truncated but slightly dorsally convex.

Holotype: Queen: AL 1.82, HL 1.62, HW 0.92, SL 0.62, EL 0.44, CI 80.3, EI 55, SI 63

Comments

This species is easily recognised by its small, light yellow workers, the large metapleural gland orifice, and the uniformly brown coloured queen with, at most, appendages and frontal part yellowish. The Sumatran specimens differ somewhat in the body coloration of the queens which is of a dark brown colour and they are larger (AL = 2.24-2.38), however, the workers are of the same yellowish appearance as the non-Sumatran specimens.

Biology and distribution

This species is known only from *Crypteronia griffithii* (Crypteroniaceae) but may inhabit another *Crypteronia* species as well (see under *crypteroniae*). A detailed account of the protective function of *maschwitzi* to its host and colonisation rates of different aged host trees are given in MOOG, DRUDE & MASCHWITZ (1998). The ants patrol young foliage and deter or kill herbivores they encounter. In addition, they clean the surface of young leaves from insect eggs. Preliminary data suggest a competitive relationship between *maschwitzi* and *crypteroniae*, the sympatric second ant partner of *Crypteronia* in Borneo and Sumatra. *Cladomyrma maschwitzi* is the most widespread *Cladomyrma* species, occurring in Borneo, Peninsular Malaysia, and Sumatra (Fig. 3-9).

Material examined

WEST MALAYSIA, Perak, Maxwell Hills (= Bukit Larut), 21.i.1988, leg. UM, #0947, ex: *Crypteronia griffithii*; Selangor, Ulu Gombak, 1990, leg. JM, #0002, ex: *Crypteronia griffithii*; EAST MALAYSIA, Sarawak, Lambir NP, Miri, 28.ii.1992, leg. BF, #92-247, ex *Crypteronia griffithii*; SUMATRA, Jambi Province, Muarabungo, Muar Buat, 18.iii.1998, leg. JM, #98-044, ex: *Crypteronia griffithii*, alt.: ca. 180 m; Jambi Province, Muarabungo, Muar Buat, 18.iii.1998, leg. JM, #98-046, ex: *Crypteronia griffithii*, alt.: ca. 180 m.

Cladomyrma nudidorsalis new species [revision of 1999]

Figures 3-2D, 3-3D

Diagnosis

Major worker: AL 0.90-1.14, HL 0.94-1.14, HW 0.81-0.94, EL 0.18-0.22, SL 0.44-0.54, CI 86-92, EI 19-22, SI 49-54 (n=4). Small body size; clypeus angulate with longitudinal striae; metapleural gland orifice small; body colour brown with mandibles and other appendages slightly lighter coloured; gastral pubescence long and dense. **Minor worker**: AL 0.76-0.88, HL 0.67-0.76, HW 0.52-67, EL 0.13-0.16, SL 0.36-0.40, CI 78-90, EI 23-25, SI 54-69 (n=7). Small body size; metapleural gland orifice small; body colour brown to light yellowish brown; gastral pubescence long and dense. **Queen**: AL 2.20-2.40, HL 1.38-1.58, HW 1.18-1.26, EL 0.46-0.49, SL 0.62-0.68, CI 80-86, EI 39, SI 53-54 (n=2). Body colour bright yellowish brown with the posterior parts of the tergites black. Clypeus gently rounded in profile, laterally distinct otherwise slightly longitudinally striate; head uniformly yellowish brown; dorsum of alitrunk without any erect hairs; metapleural gland orifice small, with a bunch of large setae in front of it; petiole low, dorsally truncated; gaster tergites 2 to 4 with erect hairs only on the posterior margin; erect hairs on gastral tergite 1 only in the anterior face and along the posterior margin.

Holotype. Queen AL 2.40, HL 1.56, HW 1.24, EL 0.50, SL 0.70, CI 86, EI 39, SI 53

Comments

This species is easily recognised in the queen's lack of erect hairs on the dorsum of the alitrunk and the very short hairs on the gastral tergites, unique characters within the genus. However, other queen characters are very similar to *petalae* (e.g., size, body colour, petiole, pubescence), and the distinction from *petalae* is mainly based on the difference of the distribution of setae, a rather variable character in *petalae*. Another trait may prove to be of importance: the workers of *nudidorsalis* tend to be of

a lighter body colour than *petalae*, but a larger sample size is needed to assess possible variation.

Biology and distribution

This is a species known from two records, one from Fraser's Hill in West Malaysia, collected in *Drypetes longifolia*, and the other from Belum, near the Thailand border, collected in *Ryparosa fasciculata* (Fig. 3-9). So far the species seems to be much less common than the syntopic *petalae*.

Material examined

Holotype: WEST MALAYSIA, Perak, Gerik, Lake Temenggor, Belum, 01.iii.1994, leg. JM, #94-086, ex: *Ryparosa fasciculata*, alt.: ca 650 m, colony size small. **Paratypes**: WEST MALAYSIA, Pahang, Fraser's Hill, 22.ii.1994, leg. JM, #94-070, ex: *Drypetes longifolia*, alt.: ca. 850 m, colony size: 660 worker in total.

Cladomyrma petalae Agosti

Figures 3-2F+G, 3-3F+G, 3-5A, 3-6A

Cladomyrma petalae Agosti, 1991: 308. Holotype queen, WEST MALAYSIA, Selangor, Ulu Gombak, 12.i.1990, leg. JM, ex: *Saraca thaipingensis*, BMNH.
Cladomyrma mossyna Agosti, 1991: 307. Holotype queen, WEST MALAYSIA, Selangor, Ulu Gombak, 01.xi.1988, leg. UM, #873, ex: *Saraca thaipingensis*, NHM. Syn. nov.

Diagnosis

Major worker: AL 0.86-1.42, HL 0.86-1.24, HW 0.78-1.16, EL 0.16-0.23, SL 0.38-0.60, CI 84-95, EI 18-21, SI 47-53 (n=18). Clypeus with longitudinal sculpture; gastral pubescence dense and regular; erect pilosity all over alitrunk, without a distinct increase on the propodeum; short erect hairs on gaster, mainly along the posterior margin of the tergites, but with scattered hairs in between; erect hairs white. **Minor worker**: AL 0.60-0.98, HL 0.63-0.86, HW 0.53-0.82, EL 0.12-0.18, SL 0.31-0.44, CI 84-95, EI 19-26, SI 48-65 (n=18). Clypeus without longitudinal sculpture, smooth; few long erect hairs on dorsal face of propodeum; very dense decumbent pubescence on gaster; body colour dark brown, with propodeum and petiole slightly brighter; small body size. **Queen**: AL 2.26-2.56, HL 1.42-1.56, HW 1.15-1.27, EL 0.46-0.54, SL 0.66-0.72, CI 81-84, EI 38-43, SI 53-59 (n=18). Dorsal part of an- and katepisternum without erect hairs (Fig. 3-6A); very flat, dorsally truncated petiole; very few erect hairs on the base of the first gastral tergite; coloration variable, even within one nest, from uniformly yellowish with darker posterior margins of the gastral tergites to completely dark brown; in most cases at least genae lighter coloured.

Holotype; Queen: AL 2.56, HL 1.51, HW 1.24, SL 0.72, EL 0.52, CI 82, EI 42, SI 58

Comments

This species is distinct from all the other species in the queen caste by the shining dorsal part of the katepisternum and the lateral part of the propodeum below the spiracle devoid of any pubescence, the small, narrow metapleural gland orifice, and the low, dorsally truncated petiole. *Cladomyrma mossyna* and *C. petalae* are now synonymized because more material is available showing a widely overlapping variation in coloration and pilosity, including the pubescence. A new inspection of the main difference between the two species, with *mossyna* having a much flatter alitrunk (AGOSTI 1991: Figs. 13 and 14), showed that this very distinct character is rather based on an artefact, with the ventral side of the alitrunk gently squashed. The correlation between this character and the size of the workers was rather coincidental based on the low number of specimens at hand at that time.

Biology and distribution

Cladomyrma petalae is restricted to the Malay Peninsula (Fig. 3-9). This species has been found in a set of six syntopic host plants, the understorey trees *Saraca thaipingensis* (Caesalpiniaceae), *Drypetes longifolia* (Putranjivaceae), *Ryparosa fasciculata* (Achariaceae) and the woody climbers *Strychnos vanprukii* (Loganiaceae), *Luvunga* sp. (Rutaceae) and *Spatholobus bracteolatus* (Papilionaceae) (MASCHWITZ et al. 1991, MOOG & MASCHWITZ 1994, MOOG et al. 2003). Despite this highly diverse host range, both field studies and extensive examination of herbarium specimens have shown that congeneric host plant species are not colonised by *petalae* (this thesis). Preliminary results of 'host acceptance' experiments with colony-founding queens collected from *Saraca* and *Spatholobus* and placed on one of the other syntopic host plants indicate that foundress queens sometimes accept an alternative host species (this thesis). However, they do not accept any other plant species with suitable internodes (controls). The mechanisms underlying this surprising queen response to particular, taxonomically diverse host plants is not yet understood and needs further study.

Water bailing is employed by workers to empty flooded nest chambers (MOOG et al. 1997). In *Saraca* (and other hosts) worker activity on the plant surface is concentrated on young developing foliage and the ants reduce herbivore damage to young leaves significantly (MOOG & MASCHWITZ 1994, this thesis). This species also precludes oviposition by female lycaenid butterflies. In addition, lycaenid larvae, even myrmecophilic ones, placed on leaf flushes and confronted with patrolling workers never survive (SEUFERT & FIEDLER 1996).

Material examined

WEST MALAYSIA, Selangor, Ulu Gombak, 23.ii.1993, leg. JM, #93-105, ex: *Strychnos vanprukii*; Perak, Cameron Highlands, Iskandar Waterfall, 12.iii.1993, leg. JM, #93-113, ex: *Saraca thaipingensis*; Pahang, Fraser's Hill, 19.ii.1993, leg. JM, #93-134, ex: *Spatholobus bracteolatus*, alt.: ca. 1,300 m, mature colony; Pahang, Fraser's Hill, 19.iii.1993, leg. JM, #93-142, ex: *Spatholobus bracteolatus*, alt.: ca. 1,300 m, colony size: ca. 630 workers; Pahang, Fraser's Hill, 14.iii.1993, leg. UM, #93-146, ex: *Ryparosa fasciculata*, alt.: 835 m; Pahang, Fraser's Hill, 24.iii.1993, leg. JM, #93-148, ex: *Ryparosa fasciculata*, alt.: ca. 830 m, mature colony: ca. 2,000 workers; Pahang, Fraser's Hill, 24.iii.1993, leg. JM, #93-149, ex: *Spatholobus bracteolatus*; Pahang, Fraser's Hill, 14.iii.1993, leg. UM, #93-157, ex: *Ryparosa fasciculata*; Pahang, Fraser's Hill, 21.ii.1994, leg. JM, #94-068, ex: *Luvunga* sp., alt.: 800 m; Pahang, Fraser's Hill, 21.ii.1994, leg. JM, #94-072, ex: *Luvunga* sp., mature colony; Perak, Gerik, Lake Temenggor, Belum, 01.iii.1994, leg. JM, #94-084, ex: *Ryparosa fasciculata*, alt.: ca. 780 m, mature colony; Perak, Gerik, Lake Temenggor, Belum, 02.iii.1994, leg. JM, #94-092, ex: *Ryparosa fasciculata*, mature colony; Perak, Gerik, Lake Temenggor, Belum, 03.iii.1994, leg. JM, #94-095, ex: *Drypetes longifolia*; Perak, Gerik, Lake Temenggor, Belum, 03.iii.1994, leg. JM, #94-105, ex: *Drypetes longifolia*; Pahang, Fraser's Hill, 22.ii.1994, leg. JM, 94-109, ex: *Drypetes longifolia*, colony size: 2,200 workers; Selangor, Genting Highlands, 22.iii.1994, leg. JM, #94-141, ex: *Drypetes longifolia*, mature colony; Perak, Bintang Mountains, Gunung Inas, 15.iii.1993, leg. JM, #93-128, ex: *Saraca thaipingensis*; Perak, Kelantan, 16.iii.1993, leg. JM, #93-129, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, leg. JM, #0004-2, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, leg. JM, #0004-4, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, leg. JM, #0004-5, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, leg. JM, #0006-1, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, leg. JM, #0006-4, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, leg. JM, #0006-5, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 1990, leg. JM, #0007, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 25.ii.1987, leg. UM, #0586, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 01.xi.1988, leg. UM, #0873, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 12.xi.1988, leg. UM, #0875, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 12.xi.1988, leg. UM, #0888, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 20.x.1988, leg. UM, #1067, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 02.i.1989, leg. UM, #1131, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 31.i.1991, leg. JM, #91-035, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, 07.i.1993, leg. JM, #93-015, ex: *Strychnos vanprukii*, colony size: ca. 300 workers, but probably same colony as #93-018, then mature colony, *Strychnos* liana climbing on *Saraca*; Selangor, Ulu Gombak, 07.i.1993, leg. JM, #93-

018, ex: *Saraca thaipingensis*, probably same colony as #93-015 (see above); Selangor, Ulu Gombak, 07.iii.1993, leg. JM, #93-111, ex: *Strychnos vanprukii*, colony size: ca. 550 workers; Perak, Gerik, Lake Temenggor, Belum, 01.iii.1994, leg. JM, #94-085, ex: *Ryparosa fasciculata*; Selangor, Ulu Gombak, 20.ii.1994, leg. JM, #94-057, ex: *Luvunga* sp., alt.: ca. 300 m, mature colony; Pahang, Fraser's Hill, 20.ii.1994, leg. JM, #94-058, ex: *Ryparosa fasciculata*, mature colony; Pahang, Fraser's Hill, 21.ii.1994, leg. JM, #94-059, ex: *Ryparosa fasciculata*, young colony: 340 workers in total; Pahang, Fraser's Hill, 21.ii.1994, leg. JM, #94-061, ex: *Ryparosa fasciculata*, probably same colony as 94-062, despite different host. Only 20 cm apart, apparently twigs have been in contact; Pahang, Fraser's Hill, 21.ii.1994, leg. JM, #94-062, ex: *Drypetes longifolia*, probably same colony as #94-061 (see above); Pahang, Fraser's Hill, 21.ii.1994, leg. JM, #94-063, ex: *Luvunga* sp. young colony: 85 workers in total; Pahang, Fraser's Hill, 21.ii.1994, leg. JM, #94-065, ex: *Luvunga* sp.; Terengganu, Sekayu Waterfalls, K. Berang, 06.iii.1993, leg. UM, #93-135, ex: *Saraca thaipingensis*; Selangor, Ulu Gombak, date?, leg. JM, 'tangle', ex: *Saraca thaipingensis*.

Cladomyrma yongi new species [revision of 1999]

Figures 3-2E, 3-3E, 3-7(3), 3-8B

Diagnosis

Major worker: AL 0.88-0.92, HL 0.86-0.92, HW 0.69-0.78, EL 0.16-0.20, SL 0.38-0.42, CI 80-86, EI 22-27, SI 52-58 (n=8). Small body size; clypeus angulate; metapleural gland orifice large; scattered hairs all over the body; hairs on propodeum not distinctly longer than those on the mesonotum; gastral pubescence short, appressed and dense; body bicoloured, with head and gaster distinctly darker than the yellowish brown alitrunk (Fig. 3-8B). **Minor worker**: AL 0.66-0.70, HL 0.62-0.66, HW 0.48-0.54, EL 0.14-0.16, SL 0.30-0.36, CI 77-84, EI 26-31, SI 60-67 (n=8). Small body size; metapleural gland orifice large; scattered hairs all over the body; hairs on propodeum not distinctly longer than those on the mesonotum; gastral pubescence short, appressed and dense; body bicoloured with head and gaster distinctly darker than the yellowish brown alitrunk. **Queen**: AL 1.80-2.06, HL 1.20-1.26, HW 0.92-1.00, EL 0.40-0.42, SL 0.56-0.60, CI 75-81, EI 40-45, SI 60-64 (n=8). Head and alitrunk evenly yellowish brown, gaster with at least the posterior parts of the tergites darker; small body size. Clypeus slightly angulate with the anterior face straight; head elongate in lateral view; genae same colour as remainder of head; dorsal part of katepisternum punctulate and with thin pubescence; metapleural gland orifice large and open; petiole in lateral view quadrangular, dorsally evenly rounded with the

posterior face gently sloped; whole body covered with long erect hairs; gaster with short, widely set subdecumbent pubescence; gaster surface with silky shine.

Holotype. Queen AL 1.86, HL 1.26, HW 0.94, EL 0.42, SL 0.60, CI 75, EI 45, SI 64

Comments

This species is characterised in the queen caste by its small size and the light yellowish brown, bicoloured coloration. The small body size might be a good character, as the type series is part of a mature colony with many alate queens and workers. This species shares its host with *hobbyi*, the latter being of close resemblance to *yongi*. However, *yongi* queens are different in three characters: their evenly yellowish brown colour, their head which is not bicoloured with the genae lighter coloured than the rest, and their petiole, which is in lateral view dorsally evenly rounded and not truncated (Fig. 3-7(3)). There probably exists a 'yellow form' of *C. yongi*, inhabiting the previously unknown, sympatric host plant, *Drypetes fusiformis*. The workers are not bicoloured but uniformly yellowish similar to *C. maschwitzi*. Whether this 'yellow form' represents a new species is briefly discussed below (see *C.* sp. nov?).

Biology and distribution

Cladomyrma yongi has only been collected in *Drypetes longifolia* (Putranjivaceae) in two localities in Sabah and Sarawak (Fig. 3-9). In ‘pruning experiments’ this species was observed to attack soft young twigs of climbers experimentally placed on the host plant, often destroying the alien plant parts in contact with the host (this thesis).

Material examined

Holotype: EAST MALAYSIA, Sarawak, Lambir NP, Miri, 26.ii.1992, leg. BF, #92-240, ex: *Drypetes longifolia*. **Paratype**: E-MALAYSIA, Sarawak, Lambir NP, Miri, 27.ii.1992, leg. UM, #92-234, ex: *Drypetes longifolia*, young colony; Sarawak, Lambir NP, Miri, 27.ii.1992, leg. UM, #92-236a, ex: *Drypetes longifolia*. **Other specimens**: EAST MALAYSIA, Sabah, Ranau, Poring Hot Springs, 09.v.1987, leg. D. Burckhardt; Sarawak, Lambir NP, Miri, 28.ii.1992, leg. UM, #92-239, ex: *Drypetes longifolia*; Sarawak, Lambir NP, Miri, 26.ii.1992, leg. BF, #92-241c, ex: *Drypetes longifolia*; Sarawak, Lambir NP, Miri, 26.ii.1992, leg. BF, #92-244b, ex: *Drypetes longifolia*.

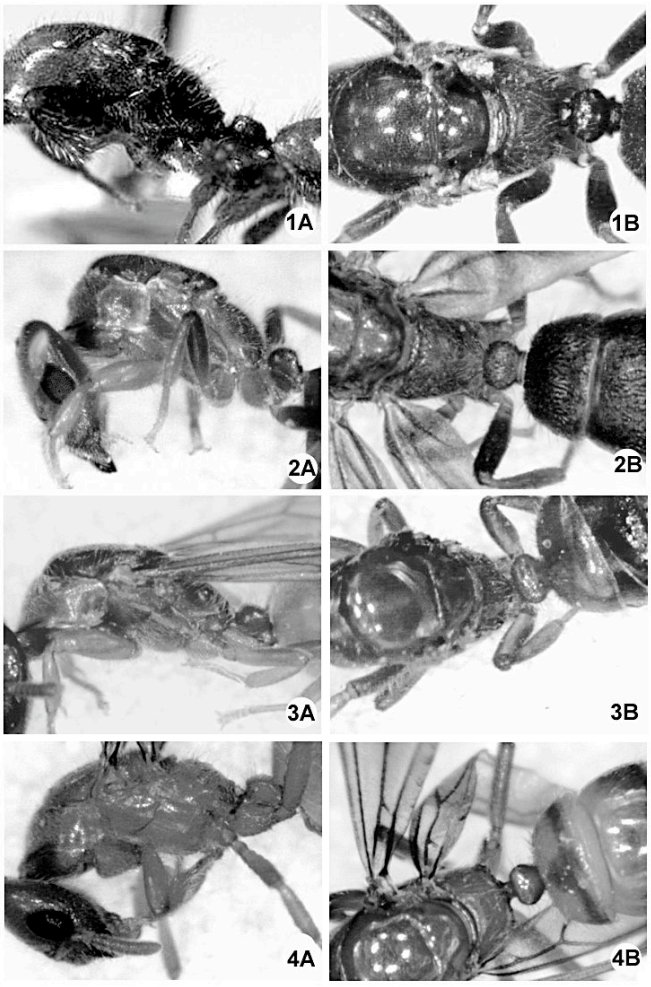


Figure 3-7: Queens of the depressed petiole group. **A** lateral view; **B** dorsal view. **1** *andrei*; **2** *maschwitzi*; **3** *yongi*; **4** sp. nov.?

Raised petiole group

Cladomyrma aurochaetae new species [revision of 1999]

Figures 3-2H, 3-3H

Diagnosis

Major worker: AL 1.04, HL 1.02, HW 0.92, EL 0.18, SL 0.48, CI 90, EI 20, SI 52 (n=1). Small body size; body colour light brown, and surface shining; clypeus in lateral view rounded, shining and not longitudinally striate; gaster cuticle thin (when prepared from ethanol, gaster collapsed); metapleural gland orifice small; gastral pubescence widely set, but hair long, longer than the space in between their insertion. **Minor worker**: AL 0.60-0.68, HL 0.62-0.66, HW 0.56-0.62, EL 0.10-0.14, SL 0.30-0.36, CI 85-97, EI 18-24, SI 50-58 (n=5). Small body size; body colour light brown, and surface shining; gastral pubescence widely set, but hairs long, longer than the space in

between their insertion. **Queen**: AL 2.36-2.72, HL 1.60-1.64, HW 1.20-1.30, EL 0.50-0.54, SL 0.76-0.80, CI 74-80, EI 40-43, SI 62-65 (n=4). Clypeus smoothly rounded with the middle part shining; head elongate in frontal view; genae, just above the mandibles, slightly reddish, head otherwise blackish; head surface shining and smooth, very widely scattered punctuation between clypeus and the ocelli; dorsal part of katepisternum shining and with a distinct pubescence; metapleural gland orifice medium sized and open, in front a bunch of long erect hairs; petiole in lateral view squamiforme, in hind view dorsally truncated; whole body covered with long erect, golden hairs; on gastral tergites 2 and 3 erect hairs only at the posterior margin; gaster tergites 2 and 3 at most with short, widely set appressed pubescence; gaster tergite 1 with long, backward curved hairs; gaster brilliantly shining; head and alitrunk evenly blackish; large body size.

Holotype: Queen AL 2.72, HL 1.64, HW 1.30, EL 0.52, SL 0.80, CI 79, EI 40, SI 62

Comments

The worker series of this species was collected from a very small colony containing only 22 workers in total. Therefore, it is likely that the extremely small soldiers and workers are the product of an early phase of colony foundation (= nanitics) and not typical for this species. This species is easily recognised by the queen's blackish and extremely shining body surface, and the distribution of erect hairs restricted to the posterior margin of the gastral tergites (the dorsal part of gastral tergites 2 and 3 lack setae).

Biology and distribution

Collected only from two localities in East Malaysia (Fig. 3-9). The first collection came from an unidentified *Neonauclea* species and *N. gigantea* in the Hose Mountains, Sarawak. The natal colony inhabited the first, single domatium of a *N. gigantea* sapling 0.42 m in height. The second collection of colony-founding queens came from a single domatium of an unidentified *Neonauclea* sp. in Kubah Park, Kuching, Sarawak.

Material examined

Holotype: EAST MALAYSIA, Sarawak, Kapit, SE side Hose Mountains, 03.ii.1997, leg. JM, #97-082, ex: *Neonauclea gigantea*, colony size small (worker = nanitics). **Paratype**: EAST MALAYSIA, Sarawak, Kapit, SE side Hose Mountains, 03.ii.1997, leg. JM, #97-088, ex: *Neonauclea* sp. **Other specimens**: EAST MALAYSIA, Sarawak, Kuching, Kubah NP, 08.ii.1997, leg. JM, #97-093, ex: *Neonauclea* sp.

Cladomyrma crypteroniae new species [revision of 1999]

Figures 3-2I, 3-3I

Diagnosis

Major worker: AL 1.12-1.28, HL 1.20-1.28, HW 1.06-1.13, EL 0.18-0.20, SL 0.48-0.58, CI 88-92, EI 17-19, SI 46-52 (n=8). Clypeus smooth, not longitudinally striate; body colour yellow; long erect hair all over alitrunk; appressed, dense gastral pubescence; large ants. **Minor worker**: AL 0.76-0.88, HL 0.68-0.80, HW 0.66-0.74, EL 0.14-0.16, SL 0.34-0.42, CI 87-95, EI 19-23, SI 53-61 (n=8). Whole body evenly yellowish; dorsum of mesonotum with many erect hairs. **Queen**: AL 2.40-2.72, HL 1.60-1.74, HW 1.34-1.52, EL 0.54-0.58, SL 0.78-0.84, CI 85-87, EI 37-40, SI 52-58 (n=8). Clypeus smoothly rounded; head slightly elongate with rounded sides in lateral view; genae same colour as remainder of head; dorsal part of katepisternum punctulate and with pubescence; metapleural gland orifice large; petiole in lateral view high, dorsally truncated with the posterior face meeting the dorsal at an angle; whole body covered with long erect hairs; gaster with long semi-decumbent pubescence, with space between the hairs as long or longer than the length of the hairs; whole body evenly yellowish, sometime with gaster slightly darker.

Holotype: Queen AL 2.64, HL 1.72, HW 1.48, EL 0.58, SL 0,78, CI 86, EI 39, SI 53

Comments

The combination of yellow body colour and smooth clypeus surface is unique among *Cladomyrma* workers. *Cladomyrma crypteroniae* workers differ from *maschwitzi* by the smooth clypeus, the higher number of ommatidiae and their smaller size, the distinctly more densely set, long pubescence on alitrunk and along the posterior margins of the gastral tergites, the darker yellow golden body colour, and the greater size of both workers and queens. As in *maschwitzi* the Sumatran material differs from the rest by having somewhat smaller and darker coloured queens with slightly longer heads (CI 82-84), showing otherwise the typical character set of *crypteroniae*.

Biology and distribution

This species was collected from *Crypteronia griffithii* in Borneo (Lambir NP, Sarawak, Danum Valley, Sabah) and in Sumatra from the Muarabungo district. Additional collections (not included here) are from Kubah Park, Sarawak and Bukit Soeharto, Kalimantan (Fig. 3-9). Both ant partners associated with *Crypteronia* (*maschwitzi* and *crypteroniae*) are the only *Cladomyrma* species which extend to Sumatra. *Cladomyrma crypteroniae* shares its host with *maschwitzi*, and preliminary data suggest *crypteroniae* to be a competitor for the host plant. In Borneo, as indicated by

herbarium material, *crypteroniae* (or *maschwitzi*) appears to be associated with another *Crypteronia* species, *C. macrophylla*, but field data are lacking. *Cladomyrma macrophylla* is restricted to the central part of Borneo and field trips to the collecting sites known from herbarium specimens have not been successful due to the rapid and destructive exploitation of formerly untouched primary forest.

Two collections (#0022, #0032) by Diane Davidson were made from a *Crypteronia* species supposed to be different from *C. griffithii* and *C. macrophylla* (D. DAVIDSON, pers. communication). However, none of the *Crypteronia* specimens, other than *griffithii* and *macrophylla*, seen by JM in several herbaria showed signs of former ant occupation, but sample size for some species was low. Lack of ant occupation, as indicated by herbarium studies, may not reflect the proportion of occupied trees in the field. For instance the very high proportion of ant inhabitation of young *C. griffithii* trees is not seen in herbar specimens because botanists usually collect plant parts from adult, flowering trees (MOOG, DRUDE & MASCHWITZ 1998). Thus, I cannot yet exclude or verify a third *Crypteronia* species as host plant of *C. crypteroniae*.

Material examined

Holotype: EAST MALAYSIA, Sarawak, Lambir NP, Miri, 30.i.1997, leg. JM, #97-073, ex: *Crypteronia griffithii*, queen. **Paratypes**: EAST MALAYSIA, Sabah, vic. Danum Valley Research Centre, 85 km W Lahad Datu, 24.vi.1991, leg. DD, #91-003; Sarawak, Lambir NP, Miri, 23.ii.1995, leg. JM, #95-083, ex: *Crypteronia griffithii*, mature colony; Sarawak, Lambir NP, Miri, 23.ii.1995, leg. JM, #95-086, ex: *Crypteronia griffithii*; Sarawak, Lambir NP, Miri, 25.ii.1995, leg. JM, #95-090, ex: *Crypteronia griffithii*, mature colony; Sarawak, Lambir NP, Miri, 26.ii.1995, leg. JM, #95-091, ex: *Crypteronia griffithii*; Sarawak, Lambir NP, Miri, 27.ii.1995, leg. JM, #95-093, ex: *Crypteronia griffithii*; Sarawak, Lambir Hills NP, Miri, 31.i.1997, leg. JM, #97-078, ex: *Crypteronia griffithii*. **Other specimens**: EAST MALAYSIA, Sabah, Ulu Segama FR, near Bole River, leg. DD, #0022, ex: *Crypteronia* sp.; Sabah, Ulu Segama FR, near Bole River, leg. DD, #0032, ex: *Crypteronia* sp.; SUMATRA, Jambi Province, Muarabungo, Muar Buat, 18.iii.1998, leg. JM, #98-047, ex: *Crypteronia griffithii*, alt.: ca. 180 m; Jambi Province, Muarabungo, Muar Buat, 18.iii.1998, leg. JM, #98-048, ex: *Crypteronia griffithii*, alt.: ca. 180 m.

Cladomyrma dianeae new species [revision of 1999]

Figures 3-2J, 3-3J, 3-5B

Diagnosis

Major worker: AL 0.89-1.29, HL 0.90-1.42, HW 0.85-1.08, EL 0.14-0.22, SL 0.42-0.58, CI 76-90, EI 16-24, SI 49-61 (n=8). Medium to large sized ants; alitrunk colour yellowish brown, with metapleuron, petiole, gaster and head dark brown; gastral pubescence short and sparse, in between the hairs longer than the length of the hair; clypeus in lateral view rounded; erect hairs on clypeus very short; head rather short; metapleural gland orifice covered with long erect setae. **Minor worker**: AL 0.76-0.84, HL 0.70-0.89, HW 0.60-0.86, EL 0.13-0.18, SL 0.36-0.46, CI 84-93, EI 19-25, SI 53-66 (n=8). Medium to larger sized ants; body colour dark brown with genae and pronotum yellowish brown; gastral pubescence short, dense, and hairs of about the same length as the distances between their insertions **Queen:** AL 2.06-2.22, HL 1.32-1.44, HW 1.12-1.18, EL 0.40-0.48, SL 0.64-0.72, CI 82-86, EI 38-41, SI 58-60 (n=8). Clypeus smoothly rounded, almost flat, in lateral view, mat, finely longitudinally striate; head elongate in frontal view; clypeus and frontal part of head reddish, head otherwise dark brown; head surface shining; dorsal part of katepisternum mat and with a distinct pubescence; metapleural gland orifice large and open, in front a bunch a long erect hairs; petiole in lateral view nodiforme to squamiforme; whole body covered with long erect, golden hairs, including all gastral tergites; gaster tergites 2 and 3 at most with short, widely set semi-decumbent pubescence; gaster tergite 1 with erect, golden hairs; gaster somewhat shining; head and alitrunk evenly dark brown to brown to light brown; large body size. **Male**: Subgenital plate long and slender, apically bicornute; small body size.

Holotype: Queen: AL 2.20, HL 1.40, HW 1.18, EL 0.48, SL 0.71, CI 84, EI 41, SI 60

Comments

This species is easily separated from all the other species by the combination of nodi- to squamiforme petiole and an abundant pilosity of erect hair on all gastral tergites. However, this species shows a considerable variation in coloration, in the shape of the petiole, the width of the alitrunk, and to a lesser extent the pilosity. Presently, it is impossible to find characters which would allow segregating this species into more than one species. Here again, all the colonies collected included only a limited number of specimens, and it is thus difficult to judge whether the workers are small or just at the beginning of the colony cycle.

Biology and distribution

Cladomyrma dianeae is recorded only from Sabah and Sarawak but increasing sampling effort is likely to extend its known distribution (Fig. 3-9). All specimens (except the holotype) were collected from several *Neonauclea* species: *N. borneensis*, *N. gigantea*, *N. longipedunculata*, *N.* sp. E (JM), *N.* sp. 1, 2 and 3? (DD) and two unidentified *Neonauclea* species (probably including *N. paracyrtopoda*). Doubtful records, which have to be verified, are from *N.* sp. C (JM). *Cladomyrma dianeae* appears to be a specialised ant associate of *Neonauclea*. It has been collected from at least 5 different *Neonauclea* species and probably colonises the three other Bornean domatia bearing *Neonauclea* as well (*N. artocarpoides, N. calcarea, N. excelsioides*). The holotype queen has probably been collected from an unknown Bornean *Fagraea* species (D. DAVIDSON, pers. comm.). All known myrmecophytic *Fagraea* species bear at the base of the petiole auricle-like scales which clasp the stem. The cavities thus formed are occupied by ants which close the entrances with carton material (BEQUAERT 1922), a behaviour not displayed by *Cladomyrma* ants. However, if this finding can be verified in future field studies it would increase the number of known host plant genera of *Cladomyrma* to eleven. I predict either that this *Fagraea* species is different from the species having ant-occupied auricles or that the colonisation by a *Cladomyrma* queen occured 'erroneously' (compare below: *Cladomyrma hewitti* ex *Myrmeconauclea strigosa*).

Material examined

Holotype: EAST MALAYSIA, Sabah, Ulu Segama FR, leg. DD, #0023 (queen), ex ?*Fagraea* sp. (Loganiaceae). **Paratypes**: EAST MALAYSIA, Sabah, vic. Danum Valley Research Centre, 85 km W Lahad Datu, 29.vi.1991, leg. DD, #91-012, ex: *Neonauclea* sp.; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 03.vii.1991, leg. DD, #91-015, ex: *Neonauclea* sp. 3?; Sabah, vic. Danum Valley Res. Centre, 85km W Lahad Datu, 06.vii.1991, leg. DD, #91-030, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 24.vi.1991, leg. DD, #91-002, ex: *Neonauclea* sp. **Other specimens**: EAST MALAYSIA, Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 27.vi.1991, leg. DD, #91-004, ex: *Neonauclea* sp.; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 27.vi.1991, leg. DD, #91-007, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 08.vii.1991, leg. DD, #91-032, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 16.vii.1991, leg. DD, #91-051, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Research Centre, 85 km W Lahad Datu, 16.vii.1991, leg. DD, #91-052, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Centre, 85km W Lahad Datu, 16.vii.1991, leg. DD, #91-053, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu,

16.vii.1991, leg. DD, #91-054, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Research Centre, 85 km W Lahad Datu, 16.vii.1991, leg. DD, #91-056, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 16.vii.1991, leg. DD, #91-058, ex: *Neonauclea* sp. 2; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 16.vii.1991, leg. DD, #91-059, ex: *Neonauclea* sp. 1; Sabah, vic. Danum Valley Res. Centre, 85 km W Lahad Datu, 22.vii.1991, leg. DD, #91-063, ex: *Neonauclea* sp. 1; Sabah, Ranau, Poring Hot Springs, 24.i.1993, leg. JM, #93-048, ex: *Neonauclea* sp. ?C; Sabah, Ranau, Poring Hot Springs, 28.i.1993, leg. JM, #93-064, ex: *Neonauclea gigantea*, young colony: 36 workers in total; Sabah, Poring, 28.i.1993, leg. JM, #93-066, ex: *Neonauclea gigantea*, mature colony; Sabah, Ranau, Poring Hot Springs, 28.i.1993, leg. JM, #93-067, ex: *Neonauclea gigantea*, colony size: ca. 1,500 workers in total; Sabah, Ranau, Poring Hot Springs, 29.i.1993, leg. JM, #93-071, ex: *Neonauclea gigantea*, young colony: 22 workers in total; Sabah, Ranau, Poring Hot Springs, 29.i.1993, leg. JM, #93-072, ex: *Neonauclea gigantea*, young colony: 14 workers in total; Sabah, road Ranau (63.5 km) - Telupid, 27.i.1995, leg. JM, #95-030, ex: *Neonauclea longipedunculata*, mature colony; Sabah, Ranau, Poring Hot Springs, 09.iii.1995, leg. JM, #95-110, ex: *Neonauclea gigantea*; Sarawak, Lambir NP, Miri, 26.ii.1992, leg. BF, #92-216 (a & b), ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 22.ii.1995, leg. JM, #95-081, ex: *Neonauclea paracyrtopoda*?; Sarawak, Niah Cave NP, Miri, 24.ii.1995, leg. JM, #95-088, ex: *Neonauclea* sp. E; Sarawak, Kapit, SE side Hose Mountains, 03.ii.1997, leg. JM, #97-084, ex: *Neonauclea borneensis*.

Cladomyrma hewitti (Wheeler) stat. rev. [revision of 1999]

Figures 3-2K, 3-3K

Aphomomyrmex hewitti Wheeler, 1910: 132. Lectotype major worker. BORNEO: East Malaysia, Sarawak, 1st Division, Bidi, .viii.1907, John Hewitt [lectotype designated by Agosti, 1991: 303; combination in *Cladomyrma hewitti*, Wheeler 1920: 53; synonym of *C. andrei*, Agosti, 1991: 303.]. MCZ. Stat. rev.

Diagnosis

Major worker: AL 0.98-1.23, HL 0.95-1.26, HW 0.84-1.06, EL 0.16-0.23, SL 0.44-0.52, CI 86-90, EI 19-23, SI 47-55 (n=8). Elongate head with subparallel sides; clypeus, in lateral view, rounded; large metapleural gland orifice; body dark brown with gaster and head distinctly darker; genae lighter brown; body surface shining; gastral pubescence sparse, widely set, so that pubescence hairs do not overlap; medium to large sized ants. **Minor worker**: AL 0.70-0.90, HL 0.66-0.84, HW 0.58-0.74, EL 0.13-0.18, SL 0.32-0.45, CI 87-88, EI 22-25, SI 55-61 (n=4). Body colour dark brown with

gaster and head darker; metapleural gland orifice large; medium-sized ant; gastral pubescence on tergites widely set and short; hairs not longer than the space in between them. **Queen**: AL 2.32-2.92, HL 1.60-1.80, HW 1.32-1.36, EL 0.52-0.60, SL 0.80-0.92, CI 77-83, EI 37-45, SI 60-68 (n=6). Head and alitrunk (dark) brown, gaster with at least the posterior parts of the tergites darker; large body size. Clypeus slightly angulate with the anterior face straight; head long in full frontal view, with parallel sides; genae same colour as remainder of head; dorsal part of katepisternum punctulate and with thin pubescence; metapleural gland orifice large and open; petiole in lateral view high, dorsally truncated with the posterior face gently sloped; whole body covered with long erect hairs; gaster with, short, widely set subdecumbent pubescence; gaster surface with silky shine.

Lectotype: Soldier AL 1.18, HL 1.22, HW 1.06, SL 0.50, EL 0.22, CI 87, EI 21, SI 47
Queen from same series as lectotype: AL 2.92, HL 1.8, HW 1.32, EL 0.60, SL 0.84, CI 73, EI 45, SI 54

Comments

After examining the type again and remounting the queen, it became obvious that the extremely long head of the worker is correlated with a unique, long, parallel-sided head of the queen, and a nodiforme petiole, which is not present in *andrei*. In lateral view the queen head of the lectotype specimen is rather elongated, correlated with an exceptionally long alitrunk. In these respects the type thus differs from all other *Cladomyrma* species. None of the additional specimens has this elongated head or AL size. However, in the non-type specimens the character combination of a long head, together with the raised petiole, make it most likely that they belong to the same species.

Biology and distribution

The type specimen was collected in Bidi (SW of Kuching, near Bau), Sarawak, in the *'swollen internodes of a shrub'* (label information). Based on current knowledge, the shrub might be a representative of one of eight domatia-bearing Bornean *Neonauclea* species, the only host tree genus of *Cladomyrma* with distinct swollen internodes whose species locally grow as shrubs (the other Bornean hosts are either understorey treelets or climbers). Indeed, new collections of this species were made only from domatia of two *Neonauclea* species. However, it cannot be excluded that the 'shrub' may belong to *Myrmeconauclea strigosa*, a small rheophytic treelet or shrub with spontaneously opening domatia. This species, regularly colonised by a variety of facultative stem-nesting ant species (MASCHWITZ et al. 1989), was never found to be inhabited by *Cladomyrma* in Sabah and Sarawak (n>50), but recent collections in

Brunei revealed that colony founding queens rarely do colonise the domatia of *Myrmeconauclea strigosa* (C. BROUAT & D. MCKEY, pers. comm.). It is not known if neighbouring *Neonauclea* trees, which often grow in *Myrmeconauclea* habitat, are the source plants of these foundress queens. A second trip to the collecting site revealed that *Neonauclea*, inhabited by *Cladomyrma* ants, grow in close vicinity to *M. strigosa* (D. MCKEY, pers. comm.) We suspect that only a very low frequency of *Cladomyrma* queens occupy the latter plant species, presumably due to high intraspecific competition for regular host plants in the vicinity. Mature colonies or alates of *Cladomyrma* were not found in *M. strigosa*. Nevertheless, this phenomenon needs to be studied in detail.

Material examined

Holotype: EAST MALAYSIA, Sarawak, 1st Division, Bidi, .viii.1907, John Hewitt, MCZ. **Other specimens**: EAST MALAYSIA, Sabah, road Ranau (60.5 km) - Telupid, 27.i.1995, leg. JM, #95-027, ex: *Neonauclea longipedunculata*, mature colony; Sabah, Tambunan, Crocker Range, 01.ii.1995, leg. JM, #95-042, ex: *Neonauclea pseudocalycina*; Sabah, road Kota Kinabalu - Tambuan (33.5 km), Crocker Range, 01.ii.1995, leg. JM, #95-047, ex: *Neonauclea pseudocalycina*, colony size small: 42 workers in total; Sabah, Tambunan, Crocker Range, 01.i.1995, leg. JM, #95-050, ex: *Neonauclea pseudocalycina*; Sabah, road Kota Kinabalu - Tambuan (39.5 km), Crocker Range, 01.ii.1995, leg. JM, #95-035, ex: *Neonauclea pseudocalycina*, mature colony.

Cladomyrma maryatiae new species [revision of 1999]

Figures 3-2B, 3-3B, 3-4B, 3-6B

Diagnosis

Major worker: AL 1.02-1.22, HL 0.98-1.08, HW 0.84-0.96, EL 0.20-0.22, SL 0.45-0.52, CI 85-89, EI 21-24, SI 51-56 (n=8). Small body size; coloration reddish brown; clypeus in lateral view smoothly curved; metapleural gland orifice large; gaster mat; gastral pubescence widely set (hairs of about the same length as the distance between their insertions). **Minor worker**: AL 0.72-0.90, HL 0.70-0.80, HW 0.59-0.67, EL 0.14-0.16, SL 0.34-0.40, CI 83-87, EI 22-29, SI 58-61 (n=8). Small body size; body colour dark brown, with head and gaster darker, and genae slightly lighter coloured; metapleural orifice covered with some long erect setae; gastral pubescence very short and dense, hair longer than the space between them. **Queen**: AL 2.10-2.28, HL 1.30-1.52, HW 1.06-1.14, EL 0.46-0.50, SL 0.64-0.74, CI 79-82, EI 42-45, SI 58-64 (n=8). Clypeus slightly angulate in lateral view, mat; head elongate in frontal view; clypeus

and frontal part of head reddish, head otherwise dark brown; head surface slightly shining; dorsal part of katepisternum mat and with a distinct pubescence; metapleural gland orifice large and open, in front a bunch of long erect hairs; petiole in lateral view squamiforme, in hind view dorsally truncated; whole body covered with long, erect, golden hairs; on gastral tergites 2 and 3 erect hairs only at the posterior margin and the lateral parts; gastral tergites otherwise at most with short, widely set appressed to semi-decumbent pubescence; gaster tergite 1 with erect, golden hairs; gaster somewhat shining; head and alitrunk evenly dark brown to brown; medium to small body size.

Holotype. Queen: AL 2.20, HL 1.43, HW 1.14, EL 0.48, SL 0.68, CI 80, EI 42, SI 60

Comments

The coloration of the queen of this species is variable, from dark brown to a lighter brown. However, this species is distinct from most others by the combination of the following characters: (i) absence of erect hairs on the second and third gastral tergite, (ii) the raised petiole, (iii) the large metapleural gland orifice, and from the very similar *aurochaetae* by the absence of the long curved hairs on the gastral tergite 1, and the mat clypeus. All the workers seen are small.

Biology and distribution

This species was collected from *Neonauclea* species (sp. C and D of JM; sp. 2 of DD) in Sabah and Sarawak (Fig. 3-9). They are recorded to display an aggressive behaviour (D. DAVIDSON, label information), a trait which it shares with most other *Cladomyrma* species (see above). [Two dubious records exist from *Spatholobus oblongifolius*, but those determinations are based solely on workers and should be regarded with some caution.]

Material examined

Holotype: EAST MALAYSIA, Sabah, Ranau, Poring Hot Springs, 14.iii.1995, leg. JM, #95-123, ex: *Neonauclea* sp., alt.: ca. 700 m, mature colony. **Paratypes**: EAST MALAYSIA, Sabah, Ranau, Poring Hot Springs, 12.iii.1995, leg. JM, #95-119, ex: *Neonauclea* sp. C, alt.: ca. 600 m, young colony: 195 workers in total; Sabah, Ranau, Poring Hot Springs, 12.iii.1995, leg. JM, #95-120, ex: *Neonauclea* sp. ?C, colony size: ca. 760 workers in total; Sabah, vic. Danum Valley Research Centre, 85 km W Lahad Datu, 07.viii.1991, leg. DD, #91-031, ex: *Neonauclea* sp. 2. **Other specimens**: EAST MALAYSIA, Sabah, Ranau, Poring Hot Springs, 24.i.1993, leg. JM, #93-045, #93-045a, ex: *Neonauclea* sp. ?C; Sabah, Ranau, Poring Hot Springs, 26.i.1993, leg. JM, #93-052, ex: *Neonauclea* sp. D, colony size: 180 workers in total; Sabah, Ranau,

Poring Hot Springs, 10.iii.1995, leg. JM, #95-114, ex: *Neonauclea* sp. C, colony size small (worker = nanitics); Sarawak, Lambir NP, Miri, 26.ii.1992, leg. BF, #92-211 a-b, ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 26.ii.1992, leg. BF, #92-212, ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 27.ii.1992, leg. BF, #92-213, ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 27.ii.1992, leg. BF, #92-215b, ex: *Neonauclea* sp.; Sarawak, Lambir NP, Miri, 28.ii.1992, leg. Alfred Buschinger, #92-223, ex: *Spatholobus oblongifolius*; Sabah, Ranau, Poring Hot Springs, 24.iii.1995, leg. JM, #95-151, ex: *Neonauclea* sp. C, colony size small (workers = nanitics).

Doubtful Species
(depressed petiole group)

***Cladomyrma* sp. nov ?**
Figures 3-7(4), 3-8A

Diagnosis

Major and minor worker: Very similar to *C. yongi*, all measurements are well within the range of *C. yongi* (see above). Small body size; scattered hairs all over the body; hairs on propodeum not distinctly longer than those on the mesonotum; body not bicoloured as in *C. yongi*, with head slightly darker and gaster same colour as the yellowish alitrunk (Fig. 3-8A); genae darker than remainder of head. **Queen**: All measurements within the range of *C. yongi*. Head elongate in lateral view; genae usually same colour as remainder of head but a few specimens with slightly darker genae; petiole in lateral view quadrangular (Fig. 3-7(4)), the anterior face meeting the dorsal at an angle, dorsally evenly rounded with the posterior face gently sloped; whole body covered with long erect hairs; gaster with short, widely set subdecumbent pubescence; head and alitrunk evenly yellowish to light brown; a few specimens with genae slightly darker than remainder of head; small body size.

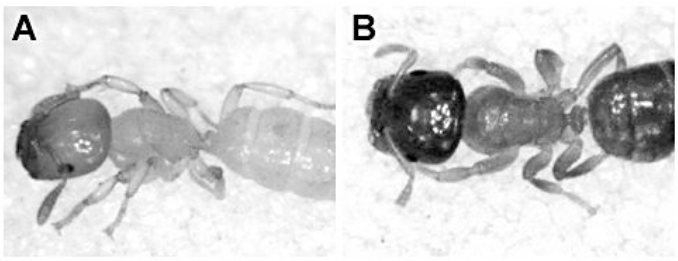


Figure 3-8: Colour variation or new species? **A** yellow major of sp. nov.?; **B** bicoloured major of *yongi* (set to same scale).

Comments

The size, coloration, and pubescence of the queen is very similar to *C*. *yongi*, but the whole body is of a slightly lighter colour than *yongi*. Most females of this probably new species, however, differ in the shape of the petiole from *yongi*. The anterior face of the petiole meets the dorsum at a sharp angle (Fig. 3-7(4)), whereas in *yongi* the transition is less well defined. However, this character shows some degree of variation, with a few specimens having petioles similar to *yongi*. The workers are extremely similar to *yongi* except in body colour which is of a more or less uniform yellowish appearance. At present, it is premature to decide on the taxonomic status of this yellow form of *yongi*, and more material is needed to assess possible variation.

Biology and distribution

The specimens were all collected from *Drypetes* species in Sabah (Fig. 3-9). In Sepilok Forest Reserve the host plant is probably *D. fusiformis*, a species not previously known to house *Cladomyrma* ants. Most herbarium material seen of *D. fusiformis* showed the typical entrance holes of *Cladomyrma*.

Material examined

Author's collection: EAST MALAYSIA, Sabah, Sandakan, Sepilok Forest Reserve, 25.iv.2000, leg. JM, #2000-027, ex: *Drypetes fusiformis* (or *longifolia*); Sabah, Sandakan, Sepilok Forest Reserve, 26.iv.2000, leg. JM, #2000-028, ex: *Drypetes fusiformis* (or *longifolia*); Sabah, Sandakan, Sepilok Forest Reserve, 26.iv.2000, leg. JM, #2000-029, ex: *Drypetes fusiformis* (or *longifolia*). **Other specimens** (now included in the author's collection): EAST MALAYSIA, Sabah, Deramakot Forest Reserve, 15.iii.1999, leg. BF, #99-036, ex: *Drypetes* sp.; Sabah, Sandakan, Sepilok Forest Reserve, 11.iii.1999, leg. BF, #99-037, ex: *Drypetes* sp.; Sabah, Danum Valley, 04.iii.1999, leg. BF, #99-039, ex *Drypetes* sp.; Sabah, Sepilok Forest Reserve, 04.iii.1999, leg. BF, #99-040, ex: *Drypetes* sp.; Sabah, Danum Valley, 04.iii.1999, leg. BF, #99-039, ex *Drypetes* sp.

3.3.4. Conclusion

This taxonomic study is a first attempt to clarify the species identities of the newly discovered *Cladomyrma* species, although limited data and taxonomic uncertainties give a rather provisional picture to date. For example, the known distribution of each *Cladomyrma* species suffers from biased sampling efforts. In particular, the central parts of Borneo could not be visited during this study. A more complete picture of the distribution of *Cladomyrma* emerges with the inclusion of host plant specimens seen in

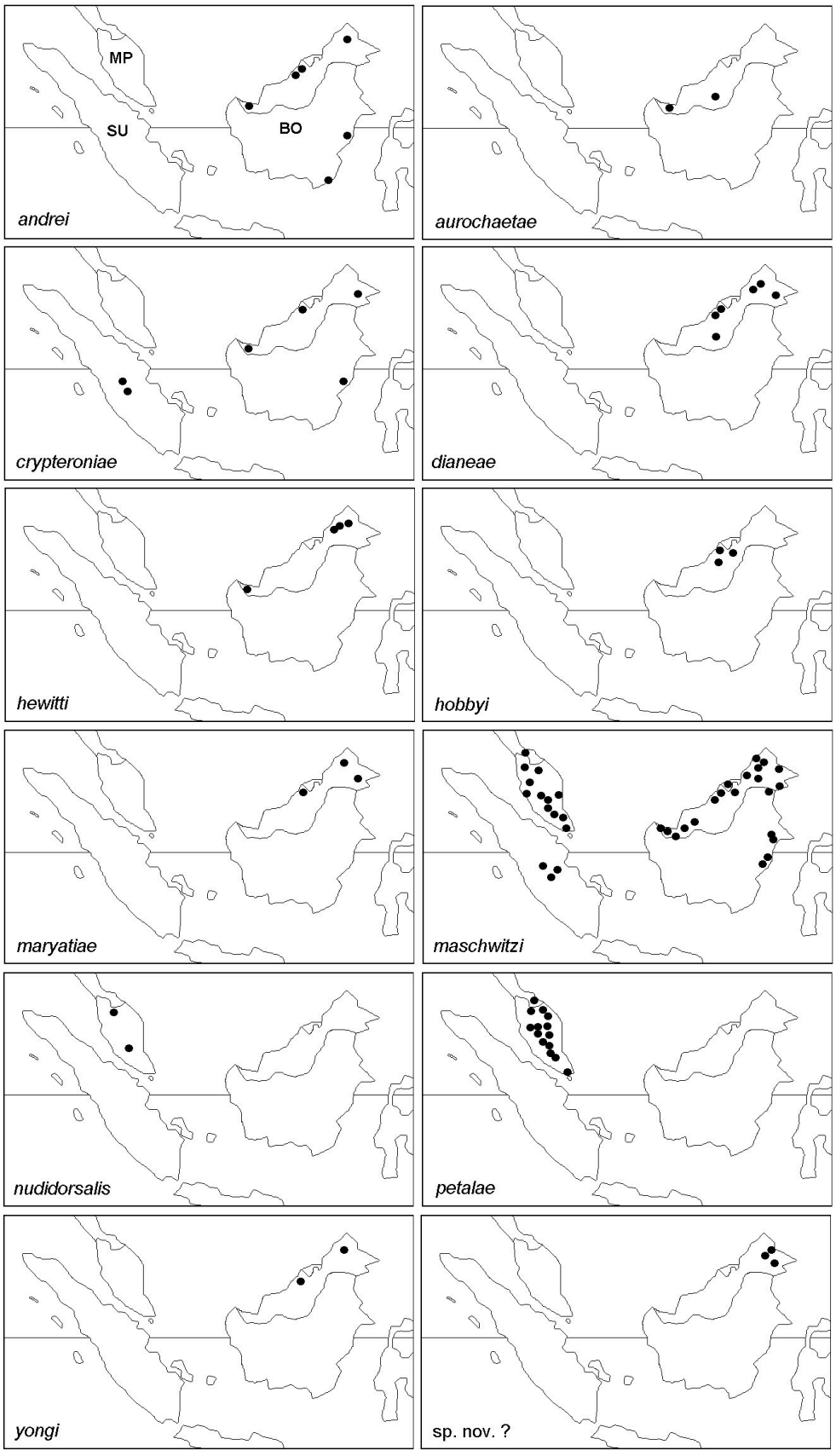


Figure 3-9: Distribution of *Cladomyrma* spp. **MP** Malay Peninsula; **SU** Sumatra, **BO** Borneo.

several herbaria for which, however, the identity of the *Cladomyrma* species could not be established. The host plant specimens showed unambiguous signs of *Cladomyrma* colonisation. Position, size and shape of the entrance holes of *Cladomyrma* are very characteristic. In addition, the remains of *Cladomyrma* workers were found in two specimens (*Drypetes longifolia*, AA 2071, leg. Ambrainsyah & Arbainsyah, 17.x.1996, Kalimantan; *Ryparosa porcata*, AA 1979, leg. Ambrainsyah & Arbainsyah, 11.ix.1996, Kalimantan). Although these worker remains were not sufficient to identify them to species level they provided evidence for *Cladomyrma* in areas which could not be visited. Species from three host plant genera not found in the field are thus known to be occupied by *Cladomyrma*. They include *Neonauclea artocarpoides, N. calcarea, N. excelsioides*, *Ryparosa porcata*, and *Crypteronia macrophylla*. Figure 3-10 provides the additional data on the distribution of *Cladomyrma* according to herbarium specimens of four host plant genera. [The herbarium data of the remaining Bornean host plant species (*Callerya nieuwenhuisii, Crypteronia griffithii*, and *Spatholobus oblongifolius*) are congruent with the localities given in Fig. 3-10 and, therefore, omitted for greater clarity.]

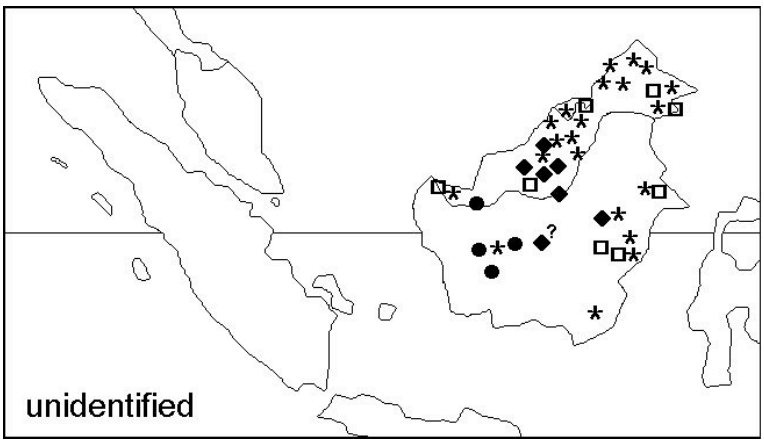


Figure 3-10: Distribution of unidentified *Cladomyrma* spp. in Borneo according to herbarium specimens of host plants. **Asterisk**: *Neonauclea* spp.; **circles**: *Ryparosa porcata*; **diamonds**: *Crypteronia macrophylla*; **squares**: *Drypetes* spp.

The distribution of *Cladomyrma* in Sumatra appears to be restricted to a rather small area (Fig. 3-9). Herbar material of *Crypteronia griffithii* was only available from the central region, and one specimen (ET 131, leg. E. Torquebiau, January 1984, Batang Ule, Jambi province) showed unambiguous signs of former *Cladomyrma* inhabitation. Its collection site in central Sumatra is very close to my own sampling sites. My efforts to find *Cladomyrma* and *Crypteronia* in other, northern parts of Sumatra were not successful. Further field trips to south Sumatra are needed to verify the restricted distributional range of *Cladomyrma* in Sumatra.

There are no indications that *Cladomyrma* occurs in other parts of the Malay Archipelago. Despite extensive herbarium studies, field trips, and a thorough literature survey, no records of *Cladomyrma* exist from the islands around Borneo, i.e., Java, Sulawesi or the Philippines. However, recent collections of *Cladomyrma* from Thailand (FUJIWARA et al. 2004) and Vietnam (YAMANE et al. 2002, EGUCHI & BUI 2006.; Fig. 3-1) indicate that species of the genus penetrate the seasonal tropical forests of Continental Asia.

Centre of *Cladomyrma* diversity is Borneo with at least nine species, followed by the Malay Peninsula with three and Sumatra with two species (Fig. 3-1). Only one species, *C. maschwitzi* inhabiting *Crypteronia griffithii*, occurs in all three geographic regions. *C. crypteroniae*, also a coloniser of *Crypteronia* trees, has been found on Borneo and Sumatra but is absent from the Malay Peninsula.

Are more Cladomyrma *species to be expected?*

Apart from taxonomic uncertainties (*C. andrei*, for example, might include several species), large areas in Sumatra and Borneo (Kalimantan) are very poorly sampled. According to herbarium studies, *Cladomyrma* is common in Kalimantan areas but species identity could not be established. I assume that field trips to these neglected regions will lead to the discovery of new *Cladomyrma* species. Likely candidates are the inhabitants of *Ryparosa anterides*, *R. porcata* and *R.* sp. nov. aff. *calotricha*, new host plants known only from herbarium specimens (own observation and WEBBER et al. 2007). The *Cladomyrma* species colonising *Drypetes fusiformis* may also represent a new species, but more material is necessary to assess possible variations (see above). An additional reason to expect additional *Cladomyrma* species from these areas is the fact that specimens of *Cladomyrma* are extremely rare in museum collections, because ant collectors who do not specifically search for host plants usually miss them due to their cryptic lifestyle. According to S. YAMANE (pers. comm.), the species collected in Thailand and Vietnam represent two or three new species. EGUCHI & BUI (2006) described a new species, *C. scopulosa*, that regularly colonises the host plant *Saraca dives*. The *Cladomyrma* species found in Thailand inhabits a host plant, *Sphenodesme* sp. (Lamiaceae), not previously known to harbour *Cladomyrma* ants (FUJIWARA et al. 2004).

3.3.5. Summary of the revision (AGOSTI, MOOG & MASCHWITZ 1999)

- the plant-ant genus *Cladomyrma* Wheeler is revised, including now eleven species
- six species are described as new: *aurochaetae*, *crypteroniae*, *dianeae***,** *maryatiae*, *nudidorsalis,* and *yongi*
- *Cladomyrma mossyna* is synonymized with *petalae*, and *cryptata* with *andrei*
- *Cladomyrma hobbyi* and *hewitti* are revived from synonymy and resurrected as species
- a key to the queen caste and a distribution map for each species is provided
- the existence of possible new species, collected from previously unknown host plants and new distributional regions, is briefly discussed; e.g., a new species from Vietnam has been described recently by EGUCHI & BUI (2006)

4. Host plants of *Cladomyrma*

4.1. INTRODUCTION

Associations of ants with plants are common phenomena in tropical rain forests. Species from over 100 genera of tropical angiosperms are known to possess specialised structures for housing ants and are termed 'ant-plants' or 'myrmecophytes' (McKEY & DAVIDSON 1993, JOLIVET 1996). These myrmecophytes offer pre-formed nesting sites (myrmecodomatia) that encourage constant associations with ants. Structures for housing ants are extremely variable ranging for example from fistulose stems over hollow thorns, shelter-forming leaves and persistent stipules to spine galleries, with each type represented by morphologically diverse examples (HUXLEY 1986, MOOG et al. 2003).

Ant-housing structures facilitate constant and long-lived associations between ants and plants and have often led to specialisation of both partners. However, because ants have the natural tendency to occupy any vacant spaces, there may be uncertainty as to precisely which plant structures are adaptations for ant occupancy. Thus, the term 'myrmecophyte' is commonly used also for plants which, in the absence of known 'specialised' structures, are continuously inhabited by ants during most of their life (DAVIDSON & McKEY 1993, LONGINO & HANSON 1995). The condition of 'regular ant inhabitation', however, is not always clear and hence may not allow to unambiguously define a plant species as being myrmecophytic or not.

Given this reservation, myrmecophytes (ant-epiphytes excluded) achieve their greatest richness in the American tropics (> 240 species; overview BENSON 1985, DAVIDSON & McKEY 1993, JOLIVET 1996). In the Neotropics, significant radiations of ant-plants occur in ten different genera, in *Acacia* (12), *Cecropia* (45-55), *Clidemia* (15-20), *Hirtella* (6), *Maieta* (ca. 15), *Ocotea* (6-10), *Tachia* (5), *Tachigali* (ca. 20), *Triplaris* (17), and *Tococa* (40-45) (McKEY & DAVIDSON 1993). In the African tropics, species richness of myrmecophytes is considerably lower (current estimate ca. 90 species) and radiations of ant-plants within genera are comparatively limited, i.e., *Acacia* (ca. 15), *Barteria* (3), *Canthium* (3-6), *Clerodendrum* (3-5), *Cuviera* (8+), *Laccosperma* (4+) and *Vitex* (4) (BEQUAERT 1922, McKEY & DAVIDSON 1993, BRETELER 1999).

Only a decade ago, the same appeared to be true for the number of myrmecophytes of both the Oriental and Australian region (McKEY & DAVIDSON 1993). Number of ant-

plants was estimated to be > 65 and > 40 species, respectively, with substantial radiations of myrmecophytes limited to the genera *Clerodendrum* (3), *Daemonorops* (4+), *Korthalsia* (7+), *Macaranga* (ca. 20), and *Neonauclea* (4+) in the Oriental region, and to the genera *Chisocheton* (6), *Kibara* (4), *Semecarpus* (4), and *Steganthera* (4) in the Australian region.

However, the relative poverty of ant-plant species in the Oriental region compared to the American and African tropics, is partly due to poor sampling efforts. While the Australian region with respect to myrmecophyte species richness is still poorly known, recent proliferation of work in Southeast Asia revealed a high number of hitherto undescribed or little-known ant-plant associations (e.g., MASCHWITZ, FIALA & LINSENMAIR 1992 and 1994a, MASCHWITZ et al. 1994b and 1996a, MASCHWITZ & FIALA 1995, WONG & PUFF 1995, FIALA, MASCHWITZ & LINSENMAIR 1996, WERNER, DUMPERT & MASCHWITZ 1996, SCHELLERICH-KAADEN et al. 1997a, FEDERLE et al. 1998a, MATTES et al. 1998, MERBACH et al. 1999, WEISSFLOG et al. 1999, JANKA et al. 2000, MOOG, FELDHAAR & MASCHWITZ 2002, RICKSON et al. 2003). Based on field and herbarium studies as well as a literature survey, MOOG et al. (2003) recognised for the Malay Peninsula alone at least 45 'true' myrmecophytic species.

The underestimation of the number of ant-plant associations in the Oriental region is also reflected in the nearly complete ignorance of the richness of 'ant-gardens', which commonly have been considered to be a phenomenon restricted to the Neotropics. Recent advances in the study of southeast Asian epiphytes, however, have shown that over 80 epiphyte species grow on ant-gardens, of which more than 60% are probably true ant-garden epiphytes, i.e., ants retrieve the seeds to their arboreal carton nests, on which the epiphytes are then cultivated (KAUFMANN et al. 2001, WEISSFLOG 2001, KAUFMANN 2002). The information now accumulating on the diversity of Oriental ant-plants may alter the hypotheses proposed to explain the differences in myrmecophyte diversity between disjunct tropical regions (DAVIDSON & MCKEY 1993).

Many of the new myrmecophytes found in the Oriental region during the last decade are host plants of the plant-ant genus *Cladomyrma* Wheeler (MASCHWITZ et al. 1989 and 1991, MOOG & MASCHWITZ 1994, MOOG, DRUDE & MASCHWITZ 1998, AGOSTI, MOOG & MASCHWITZ 1999). To our present knowledge, *Cladomyrma* inhabits 24 species of host plants in 10 different genera and eight families. The following chapter provides a species-level overview of all *Cladomyrma* host plants known from Borneo, the Malay Peninsula and Sumatra, including descriptions of ant-housing structures, ant inhabitant identity, onset of colonisation during plant ontogeny, nest structure, occupancy rate, and considerations of results obtained from herbarium specimens.

The present contribution aims at summarising and completing the scattered records of *Cladomyrma* host plants (including the ant partners) and at assessing both the regularity of ant association and the degree of morphological specialisation toward myrmecophytism.

4.2. MATERIAL AND METHODS

Field studies

A survey of host plants of *Cladomyrma* was conducted in a total of over 200 sites in Malaysia (Peninsula and Borneo) and in Sumatra. Additional information came from a few sites in Kalimantan (Indonesia, Borneo). The main study sites are presented in figure 4-1.

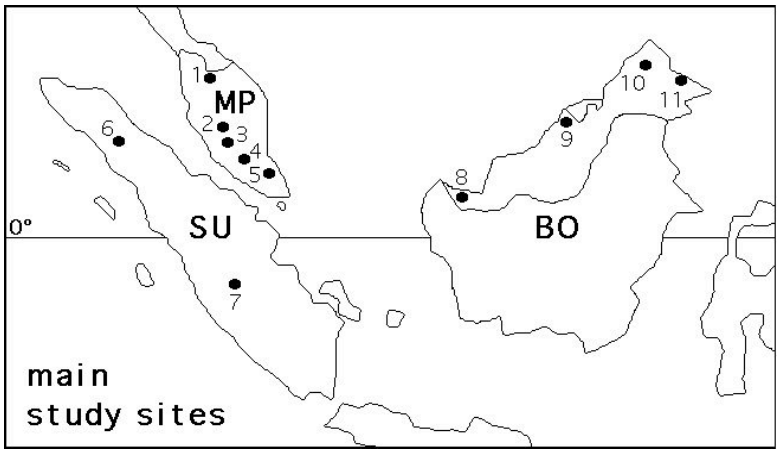


Figure 4-1: Main study sites on the Malay Peninsula (**MP**), Sumatra (**SU**) and Borneo (**BO**): **1**. Belum, Gerik, Perak, 5°31'N 101°25'E; **2**. Fraser's Hill, Raub, Pahang, 3°43'N 101°44'E; **3**. Ulu Gombak, Selangor, 3°19'N 101°45'E; **4**. Pasoh Forest Reserve, Negeri Sembilan, 2°58'N 102°18'E; **5**. Endau-Rompin NP, Pahang/Johore, 2°25'N 103°20'E; **6**. Gunung Leuser NP, Aceh, 3°50'N 97°30'E; **7**. Sg. Busaha, Muaranungo, Jambi, 1°41'S 101°49'E; **8**. Kubah Park, Kuching, 1st Div., Sarawak, 1°33'N 110°12'E; **9**. Lambir Hills NP, Miri, 4th Div., Sarawak, 4°12'N 114°01'E; **10**. Poring Hot Springs, Ranau, Sabah, 6°03'N 116°41'E; **11**. Sepilok, Sandakan, Sabah, 5°50'N 117°55'E.

In each site, the following characters were studied: plant size and ant occupancy (either by *Cladomyrma* or other ant species; including presence of colony foundations). Plants of all sizes were examined to determine when ant colonisation occurs and if it continues during the life of the host plant. For a subset of these plants, characteristics of domatia (if present), ant colony size, number of entrance holes and nest chamber length (as proportion of total stem length) were measured. For the tree *Saraca thaipingensis*, re-colonisation experiments were conducted. This species resprouts easily from cut stumps, allowing the observation of repeated ant

colonisations. Ant collections were preserved in 75-80% ethanol and later identified in the laboratory, following the revision of *Cladomyrma* (AGOSTI, MOOG & MASCHWITZ 1999) or, for other ant taxa, the keys of HÖLLDOBLER & WILSON (1990) and BOLTON (1994).

Herbarium studies

With few exceptions, plant specimens were collected from non-fertile individuals because ants colonised plants early in their ontogeny. Nevertheless, almost all host plants of *Cladomyrma* could be identified to species level by comparing dried specimens with herbarium material at several institutions: Forest Research Institute Malaysia, Kepong (KEP), Forest Research Centre, Sepilok, Sandakan (SAN), Nationaal Herbarium Nederland, Leiden (L), Royal Botanic Gardens, Kew (K) and Phillippine National Herbarium, Manila (PNH). Identification of host taxa belonging to the genera *Luvunga* and *Neonauclea*, however, was exceptionally difficult (for details see under the respective paragraphs below). In order to verify ant colonisation of *Cladomyrma* host plants in areas that could not be visited I systematically examined herbarium material from the herbaria K, KEP, L, PNH and SAN. Entrance holes of *Cladomyrma* are usually distinguishable from those made by other ant species or stemborers by their size, regular shape with clearly defined margins and regular distribution along the twigs. In addition, I checked the labels accompanying herbarium specimens for mentioning of ant occupation, however, most collectors failed to note this conspicuous trait. Few collections provided precise geographic coordinates but coordinates of most collection localities could be determined using gazeteers or topographic maps.

Greenhouse studies

It could be postulated that domatia (swollen twigs) observed in some host plants of *Cladomyrma* are environmentally (induced by ants or other insects) rather than genetically based and thus have to be considered as galls. As a partial test of this possibility, some ant-free host plant species were grown as saplings or rooted cuttings in greenhouses both at Frankfurt University, Germany, and at the Ulu Gombak Field Station, Malaysia, until they produced domatia.

Voucher specimens

Dried specimens of host plants are deposited at L; acccession numbers are AMO-001 to AMO-151. Additionally, alcohol material (100% ethanol) is available at L for the following *Neonauclea* herbarium specimens: AMO-033, AMO-065 to -067, AMO-069, AMO-071, AMO-081 to -083, and AMO-085 to -089.

4.3. RESULTS

4.3.1. Fabaceae - Caesalpinioideae

Saraca thaipingensis Cantley ex Prain

Figures 4-2, 4-5, 4-8

Tree to 25 m; locally common; in forests, mostly in stream valleys, growing along rocky banks; lowlands up to 1,100 m altitude (HOU, LARSEN & LARSEN 1996). The tributaries and headwaters in Peninsular Malaysia are often so densely bordered by *S. thaipingensis*, thus forming tunnels through the forest, that CORNER (1988) coined the term '*Saraca*-streams'. Distribution: Malay Peninsula (throughout), West and Central Java; few collections north of the Kra Isthmus (South Burma and North Thailand).

Ant-housing and other ant-related structures: The twigs of *S. thaipingensis* do not provide swollen parts or 'weak spots' (so-called prostomata) to promote ant inhabitation and access, yet they have internodes increasing in diameter towards the nodes (Fig. 4-2B) which support the big-sized pinnate leaves (petiole and rachis up to 60 cm long; Fig. 4-2A). The pith of young internodes is relatively soft but does not degenerate to create a cavity (Fig. 4-2D). The margins of young leaflets bear 1 to 3 active extrafloral nectaries (EFN) which attract a diversity of non-resident ants (e.g., *Camponotus*, *Crematogaster*, *Gnamptogenys*, *Rhoptromyrmex*, *Tapinoma*, *Technomyrmex*). In contrast, the obligate ant partner *Cladomyrma* exploits the EFN only under starving conditions. Flushes of newly developed leaves are characterised by delayed greening (Fig. 4-2C). Young leaves are preferentially patrolled by *Cladomyrma* ants, resulting in a significant reduction of young leaf herbivory (MOOG & MASCHWITZ 1994 and 2000, this thesis).

Ant inhabitants: The association with *Cladomyrma petalae* ants was first reported by MASCHWITZ et al. (1991). The association has been found in all parts of the Malay Peninsula from southern Thailand to Singapore. In small, restricted local habitats, *C. petalae* may be replaced mainly by a particular *Crematogaster* species (sp. 1) which facultatively nests in a wide variety of plant species (see below). Occasionally, species of other ant genera can be found in abandoned *Cladomyrma* chambers, stem borer cavities or dead twigs (*Camponotus*, *Monomorium*, *Pheidole*, *Tapinoma*, *Technomyrmex*, *Vombisidris*).

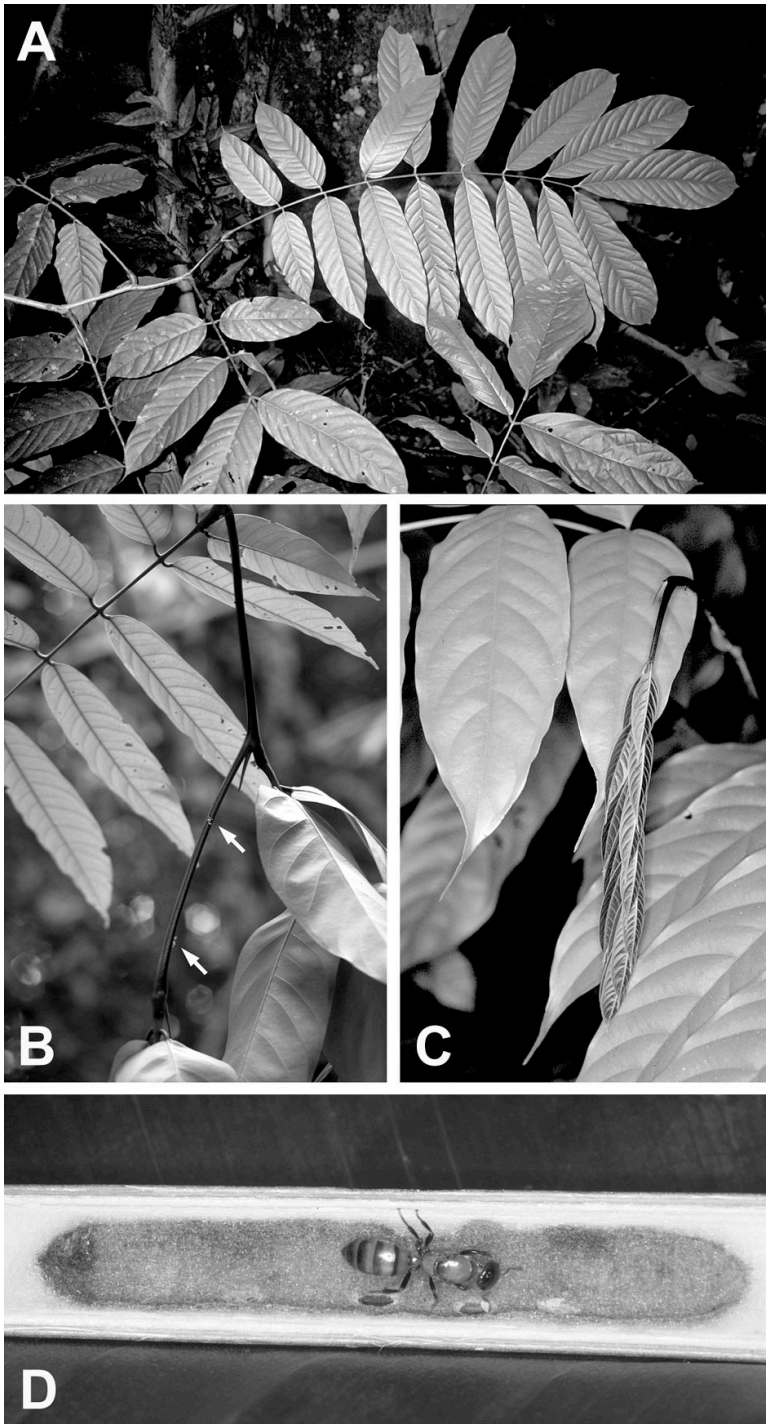


Figure 4-2: *Saraca thaipingensis*. **A**: twig and pinnate leaf of an ant-inhabited sapling; **B**: young internode with two *Cladomyrma* colony foundations. Pith is pushed out through the entrance holes by the foundresses (arrows); **C**: young purple leaf flush which dangles for several days before stiffening and straightening; **D**: dissected internode showing a founding chamber (length 2.8 cm) of a *Cladomyrma petalae* queen. The inner walls of the chamber turn brown shortly after excavation of the cavity.

Onset of ant occupation: Colonisation of saplings usually starts in plants ≥ 1 m in height because only then the primary stem diameter is sufficient to allow accomodation of *Cladomyrma* founding females. On average, the internode diameter at point of entry was 5.7 mm ± 1.06 SD (range 3.8 to 9.8 mm; n=118). *Cladomyrma* foundresses are the primary colonisers of *Saraca* trees. The founding females of other ant taxa (e.g., *Crematogaster* sp. 1) lack the ability to create cavities in *Saraca* twigs and they rely on the presence of preformed shelters such as stipules or cavities chewed by *Cladomyrma* or other stem-boring insects. Support for the 'priority effect' of *Cladomyrma* comes from the re-colonisation experiments (Tab. 4-1).

Table 4-1: Re-colonisation experiments on *Saraca thaipingensis* growing in open, sunny habitat (n=6). All branches and twigs of tree stumps (> 15 cm in diameter) were cut back to initiate resprouting. After one to 25 months the newly produced sucker shoots were dissected and examined for ant inhabitants. *Foundations* = foundress queen still without workers but brood may be present; *Natal colony* = the initial founding chamber is not yet enlarged by the nanitic workers and only one nest entrance hole is present; *young colony* = more than one internode colonised but alate sexuals not yet produced (ergonomic stage); *mature colony* = alates present (reproductive stage). *Superscript* = [1] overgrown by vines, only few shoots produced; [2] the foundations were all found on two shoots not yet patrolled by the mature colony; [3] three young colonies had taken over neighbouring foundations; [4] *Monomorium* inhabited an abandoned *Cladomyrma* foundation chamber; [5] *Technomyrmex* nested between leaflets; [6] *Technomyrmex* inhabited dead wood at the tree stump outside the patrolling range of *Cladomyrma*.

time	*Cladomyrma petalae*				other nesting
[month]	no. of foundations (dead)	no. of natal colonies (no. of workers)	no. of young colonies (no. of workers)	no. of mature colonies (no. of workers)	ant taxa
1	1	0	0	0	
9	5 (1)	1 (39)	1 (116)	0	
10[1]	10 (5)	0	0	0	*Monomorium* [4]
13	23 (11)	1 (4)	5 (58 to 460)[3]	0	*Technomyrmex* [5]
24	0	0	2 (9, 34)	1 (~ 4000)*	
25	7[2]	1 (11)	0	1 (~ 5500)*	*Technomyrmex* [6]

* Note that colony growth of *Cladomyrma* in the re-colonisation experiments is not typical for colony growth in *Saraca* saplings. The sun-exposed tree stumps produced unusually high numbers of new sucker shoots within a short time period, thus growth of the colony was not restricted by limited nesting space or food shortage (young shoots function as substrate for scale insects).

Mutiple foundations of *Cladomyrma petalae* occured shortly after production of the first new shoots. Several young colonies developed during the first year after start of the experiments and apparently initiated a phase of intense intraspecific competition. Eventually, only a single colony managed to get established on the host and other foundations or ant species, if present, were restricted to plant parts outside the

patrolling range of the 'winner' colony. This colonisation process is typical for all *Cladomyrma* species, irrespective of host taxon.

Ant occupancy rate: Occupancy rates of *Saraca thaipingensis* can vary due to tree age (tree size), habitat and interspecific competition. For example, of the 280 *Saraca* trees located at Ulu Gombak in an area of about 2000 m^2, 53% were occupied by *Cladomyrma petalae*, while 37.5 harboured *Crematogaster* sp. 1 (Fig. 4-3). *Saraca* trees inhabited by *Crematogaster* sp. 1 were predominantly found at the river bank in a small strip of ca. 5 m width on both sides along the river, and colonisation rate reached 70% in the river bank strip. In contrast, trees inhabited by *Cladomyrma* were mostly found away from the river bank deeper in the forest, and there occupancy rate was 86%. This difference in occupation pattern between the two ant species corresponded not only to habitat type (river bank versus forest) but also to differences in height of occupied trees because *Saraca* trees at the river bank are, on average, taller than those of the forest. Overall, *Crematogaster* sp. 1 was found in a significantly larger proportion of taller trees (Mann-Whitney U-test, $P < 0.0001$). If only trees of 1 to 10 m height are considered, colonisation rate by *Cladomyrma* reached almost 90%.

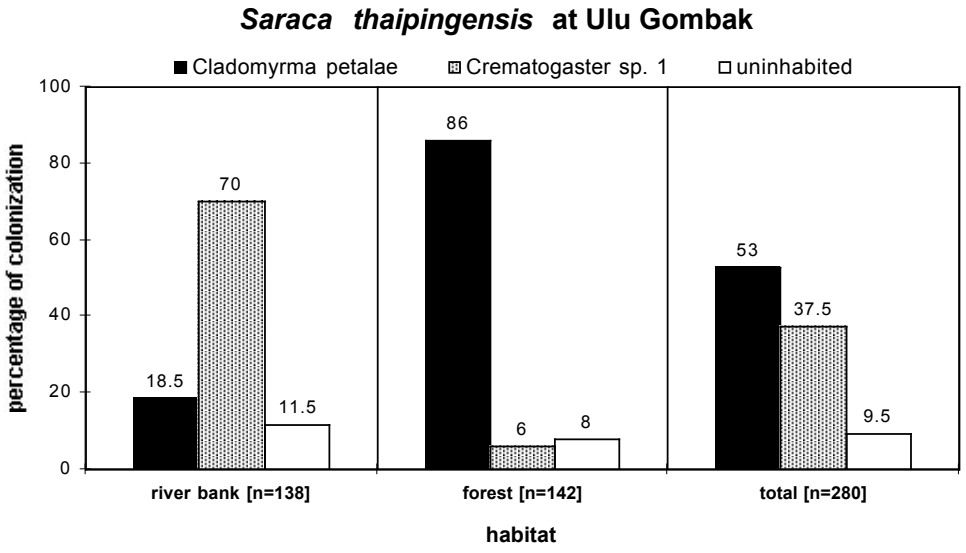


Figure 4-3: Ant occupancy of *Saraca thaipingensis* (n=280) in a 2000 m^2 study site at Ulu Gombak in relation to habitat. *River bank* = 5 m wide strip along each side of the river; *forest* = the study area up to 100 m into the forest, excluding the river bank.

Crematogaster sp. 1 ants are abundant at river and forest fringes and once they are established at one site they mostly prevent the colonisation of a *Saraca* by colony-founding *Cladomyrma* queens. Any *Cladomyrma* foundress encountered on the plant will be chased away or killed by the *Crematogaster* workers (RIEDEL 1997, pers. observation).

Differential use of *Saraca* by *Cladomyrma* and *Crematogaster*: The myrmicine species *Crematogaster* sp. 1 is not specialised to living in a particular host plant but uses many plant species in an opportunistic way (e.g., *Ardisia* sp., *Callerya* (*Millettia*) *atropurpurea*, *Knema* sp., *Lepisanthes tetraphylla*, *Pometia pinnata*, *Tetrastigma dubium*, *Trigonostemon malaccanus*, and *Vernonia arborea*). A mature *Crematoagster* sp. 1 colony often extends over several neighbouring plants (polydomy), usually with only a small part of each plant occupied. The workers are able to cut small chambers into internodes, however, the entrances are somewhat irregular in shape and size (Fig. 4-5D, Fig. 4-6) and the nodes are not perforated (Fig. 4-4), resulting in a nest structure of many separated small chambers distributed over several plants.

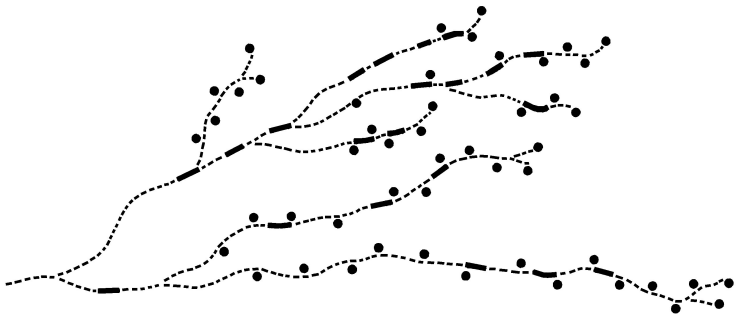


Figure 4-4: Schematic illustration of nest chambers of *Crematogaster* sp. 1 in a *Saraca* branch. *Broken line*: branch sections without nest cavities; *solid bold line*: nest chambers, confined to one internode; *solid circles*: attachment of leaves (usually one leaf per internode, at least towards the twig apices).

In contrast to the true plant-ant *Cladomyrma*, the *Crematogaster* sp. 1 foundress lacks the ability to chew a founding chamber into a young stem or twig. She relies on shelters like stipules or hollows gnawed by *Cladomyrma* or other stem-boring insects to found a colony (Fig. 4-5A-C). This has important consequences for the establishment of a *Crematogaster* colony on a *Saraca* tree. In saplings, *Cladomyrma* is usually the first occupant and attains a monopoly over the host plant, preventing the colonisation by *Crematogaster* foundress ants. Despite this 'priority effect', small *Cladomyrma* colonies may secondarily be displaced by *Crematogaster* species when workers of a mature *Crematogaster* colony enlarge their territory onto a neighbouring *Saraca*. In staged encounters between similar-sized colonies of a *Crematogaster* sp. 1 and *C. petalae*, the latter successfully defended its host plant against invasion by *Crematogaster* ants (n=5; unpublished results). However, when colony size of *C. petalae* was distinctly smaller (about half size) than that of *Crematogaster* sp. 1, the *Cladomyrma* colony was evicted and killed (n=6).

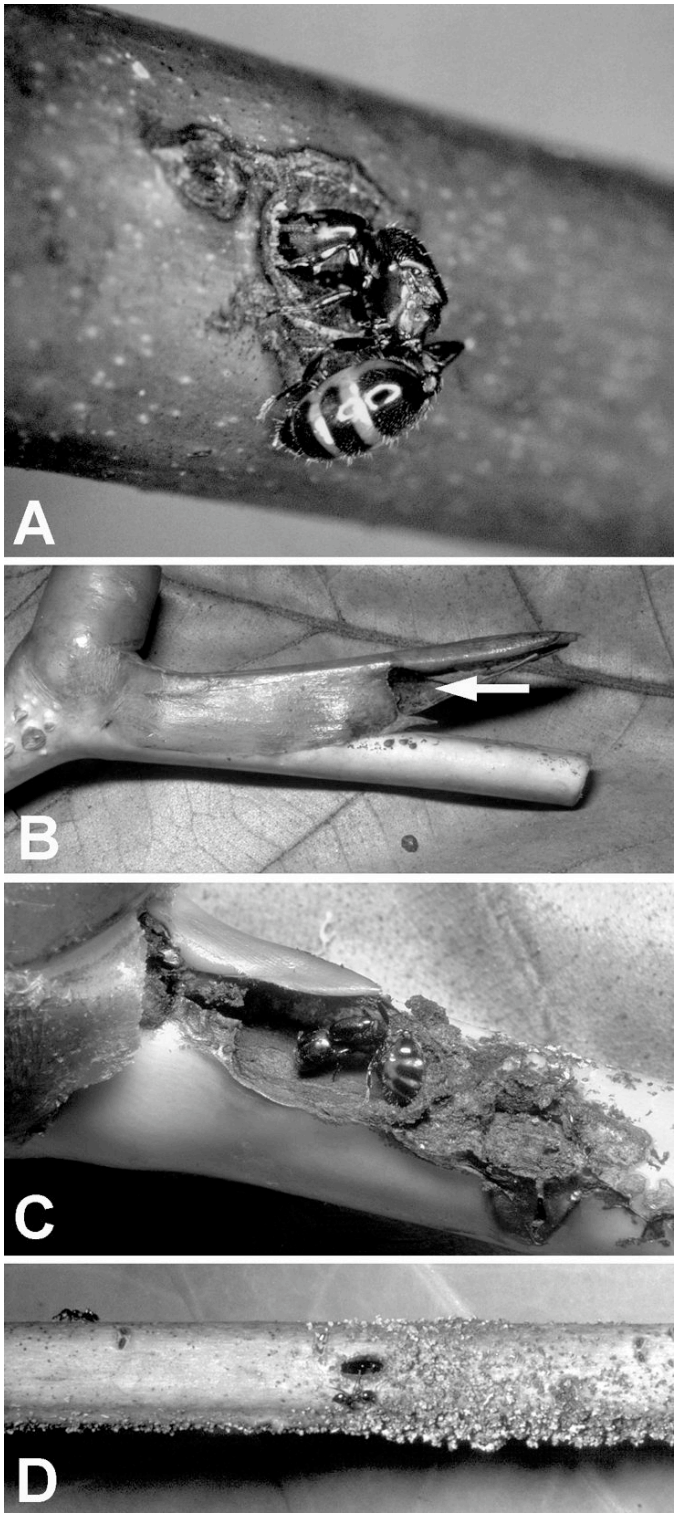


Figure 4-5: *Crematogaster* sp. 1 colonising *Saraca thaipingensis*. **A**: a foundress trying to enter a *Cladomyrma* founding chamber by removing the pith with which the entrance hole is plugged; **B**: a stipule with exit hole (arrow) tightly clasping an internode; **C**: stipule removed, showing a *Crematogaster* foundress in the depression produced by a herbivorous insect; **D**: slit-like entrance hole in an internode inhabited by *Crematogaster* workers. Excavated pith debris is smeared onto the internode surface.

Several traits distinguish the plant-ant *Cladomyrma petalae* from the arboreal generalist *Crematogaster* sp. 1: (i) *Cladomyrma* founding queens are very efficient at finding their host and tunnelling cavities into living plant tissue (resulting in priority of access); (ii) host specificity is more or less strongly developed; (iii) the ant colony stays on the plant throughout the life of the colony (host fidelity) and workers do not forage off their host; and (iv) strong intraspecific competition for host plants (multiple colony foundations on an individual plant).

With respect to *Saraca thaipingensis*, these differences between a specialist and a generalist ant species are also reflected in the type of nest construction. *C. petalae* workers chew entrance holes of similar size and shape whereas those produced by *Cr.* sp. 1 are strongly variable (Fig. 4-6). This trait is probably linked to a more efficient defence of the nest in *Cladomyrma* ants which, in contrast to polydomous *Cr.* sp. 1, cannot give up nest parts in encounters with competing ants without endangering colony survival as a whole. [Entrance hole dimensions are also very helpful in assigning *Cladomyrma* colonisation to *Saraca* herbarium specimens.]

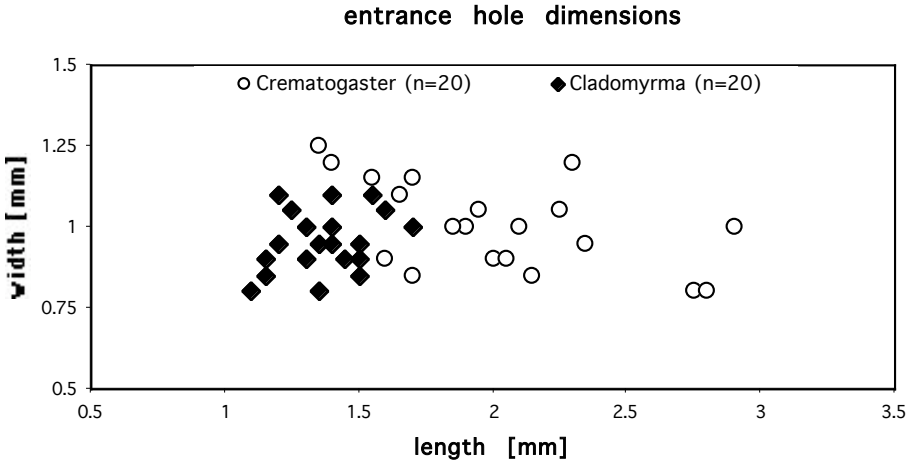


Figure 4-6: Comparison of entrance hole size and shape between *Cladomyrma petalae* and *Crematogaster* sp. 1 nesting in *Saraca thaipingensis*.

The most important difference in nest structure between *C. petalae* and *Cr.* sp. 1 is found in the distribution of nest chambers within a plant. In contrast to *Cr.* sp. 1, *C. petalae* ants hollow out *Saraca* stems and twigs throughout their length and perforate the nodes, thus the nest communicates internally with every branch and twig and forms a continuous tunnel system (Fig. 4-7). Disconnected nest parts are rare and can usually be bridged by crossing the surface of one internode only. This allows nest

maintenance, such as dispersal of food, brood and scale insects, to take place within the safety of the hollow stems. Principally, other *Cladomyrma* species, living on other host taxa, build the same type of nest, at least in adult plants. The situation, however, is different in young saplings of *Callerya*, *Drypetes* and *Spatholobus*, and in young and adult *Neonauclea* host plants. Here, the colonies live in a series of dispersed domatia with exposed routes connecting them (see below).

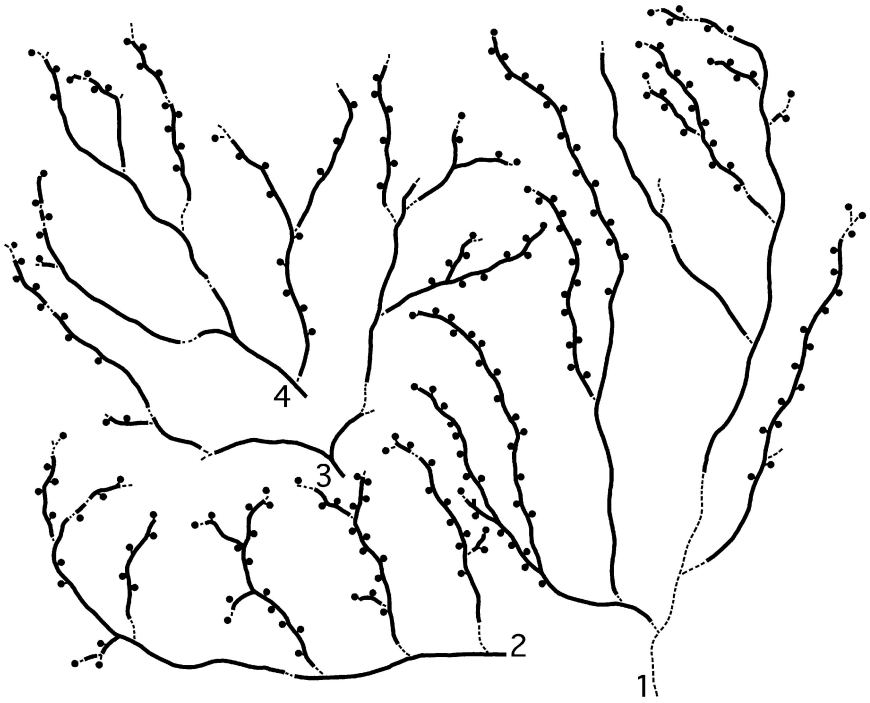


Figure 4-7: Schematic illustration of nest chambers of *Cladomyrma petalae* in the four main branches of a *Saraca* tree 8.2 m in height. Total length of branches and twigs 44.3 m, with 35.9 m (81%) used as nest chamber. *Broken line*: branch sections without nest cavities; *solid bold line*: nest chambers extending over many internodes to form a more or less continuous nest system; *solid circles*: attachment of leaves (usually one leaf per internode, at least towards the twig apices).

The regularity of nest structure in *C. petalae* is exemplified by the dissection of a young, still non-ramified *Saraca* tree (Fig. 4-8). Here, the pith of the entire stem is removed, except for a short section in the upper third. Pith not removed during or shortly after internode development becomes hard and woody and may form a barrier disconnecting nest parts throughout the life of the colony. However, workers are able to gnaw off woody pith and the barrier may be removed gradually. Entrance holes are evenly distributed, one in each internode.

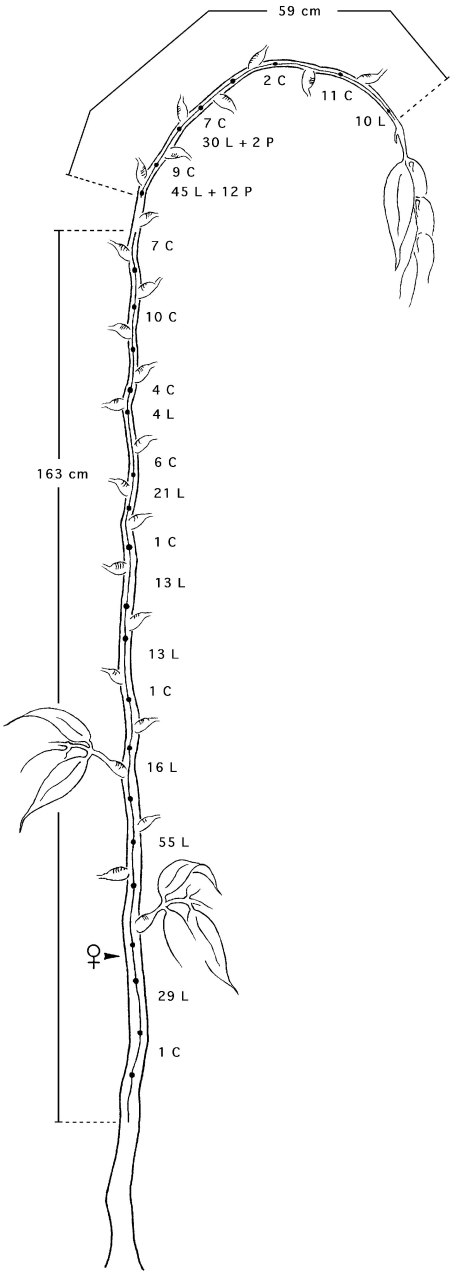


Figure 4-8: Nest structure of *Cladomyrma petalae* in a young, non-ramified *Saraca thaipingensis*. The stem of a 3 m tall tree was cut and dissected in its entirety. For each segment, the number of larvae (L), pupae (P) and coccoids (C) was counted. In total, the colony contained 640 workers, 236 larvae of different stages, 12 pupae and 59 coccoids (mostly Pseudococcidae, but also some Coccidae). The colony had not yet produced alate sexuals. The female symbol is where the physogastric colony queen was found. Solid black circles indicate the 27 entrance holes (for more clarity all facing the observer). The total nesting space (2.22 m) consists of 2 nest chambers, 163 and 59 cm in length.

The queen is mostly found in the lower quarter of the nest, probably because this is the most protected part of the plant. In Southeast Asia, some predators of ants torn open stems of ant-plants to search for prey (FEDERLE et al. 1999). Also, after physical

disturbance of the host plant (by wind storm and fallen trees) that lead to loss of stem parts, the ant queen is more likely to survive in the lower part of the plant and – provided the host possesses a high ability to resprout– allows the recovery of the ant colony. The majority of trophobiotic scale insects tended by *Cladomyrma* is usually found in the younger parts of the host, but a few coccoids are also present in the lower part of the tree trunk.

Herbarium study: The examination of 86 herbarium specimens of *Saraca thaipingensis* corroborated the result on ant occupancy obtained from the field. *Cladomyrma* inhabitation could be assigned to 42% of the specimens. For another 22%, hollow twigs or entrance holes could not unambiguously attributed to *Cladomyrma* or other ants such as *Crematogaster* sp. 1. The remaining specimens (36%) lacked signs of ant occupancy. All specimens seen from Java (n=9) belong to the latter group, a region where *Cladomyrma* does not occur (Fig. 3-1).

Generally, occupancy rates derived from herbarium studies are lower than those observed in the field due to several reasons. First, botanists usually collect fertile specimens and ant inhabitation may be less pronounced or lost in flowering plants (see below for *Crypteronia*). Second, twig sections collected are often very short and may not show the hollows and entrances which may be present in other parts of the plant. Third, botanists rarely mention ant occupation and, by failing to recognise the regularity of ant colonisation, often regard ant tenants as irregular parasites. For example, only two labels of ant-inhabited *Saraca* specimens (n=36) mentioned the occurrence of ants in the twigs and branchlets (FRI 29421, leg. KOCHUMMEN, and MAXWELL 78-288).

Saraca dives Pierre

Figure 4-9

Tree to 20 (25) m; in dense or sparse forests, river sides, along valleys, by streams; lowlands up to 1,000 m altitude. This species closely resembles *S. thaipingensis* in habit but it is, among others, distinguished by the number of stamens, larger anthers, and persistent bracteoles (ZUIJDERHOUDT 1968). The flowers are remarkably large, yellow and showy, the plant is thus often cultivated as an ornamental. Distribution: South China (Guangdong, SE and SW Guangxi, SE Yunnan), Laos, Vietnam. Note: Not seen in the field.

Figure 4-9: Stamp showing inflorescence of *Saraca dives*, Vietnam.

The association of *S. dives* with the newly described *Cladomyrma* species, *C. scopulosa* EGUCHI & BUI, has been recorded from North Vietnam (EGUCHI & BUI 2006). Young shoots and branches of *S. dives* are frequently colonised by *C. scopulosa*. Interestingly, this ant taxon is the only one in the genus which may exhibit a polygynous colony structure (EGUCHI & BUI 2007).

After introducing the authors to the association of *S. thaipingensis* with *C. petalae* in Ulu Gombak, Malaysia (Nov. 2005), the authors were suprised of the apparent similarities between the two associations. Habitat and ant-housing structures of *Saraca dives* studied in the Cuc Phuong NP, Vietnam, are remarkably similar to *S. thaipingensis*. In addition, *Cladomyrma scopulosa*, the inhabitant of *Saraca dives*, closely resembles *C. petalae* but differs in having a characteristic shape of the clypeus (EGUCHI & BUI 2006).

It is not known, at present, whether *S. dives* is colonised by ants in other parts of its distribution. The examination of herbarium material in Leiden revealed that two of three specimens, all collected in North Vietnam, had hollowed twigs with one entrance hole typical of *Cladomyrma* (CHEVALIER 30195, POILANE 16580). The collection labels did not mention ant occupation.

4.3.2. Fabaceae - Papilionoideae

Callerya nieuwenhuisii (J.J. Sm.) Schot

Figures 4-10A-C, 4-11, 4-12

Woody climber, up to 45 m; locally common; in mixed dipterocarp and slightly swampy forest, often near rivers, flatland to steep slopes; lowlands up to ca. 1,300–1,400 m altitude (SCHOT 1994). Distribution: Borneo (Brunei, Kalimantan, Sabah and Sarawak).

Ant-housing structures: Young lianas < 6 m in length develop swollen internodes (Fig. 4-10B). The primary outer diameter of these domatia is increased by ca. 1 to 2 (rarely 3) mm in relation to the previous internode. This corresponds to an increase of the pith canal which is later hollowed out by ants (Fig. 4-10A). This initial increase in diameter slowly decreases over ca. 2 to 3 following internodes. In young plants, the first domatia usually develop in a height between 1 to 1.5 m. In older plants, the primary diameter of the stem increases at each branching event (Fig. 4-10C). Although the basal internodes of a branch exhibits a similar increase in diameter as young-plant domatia, they appear less 'swollen'. The diameter of the nest chamber within domatia and basal internodes is, on average, 3.8 mm (n=10), those of 'normal' internodes 2.1 mm (n=10). Prostomata are not provided.

Ant inhabitants: The Bornean woody climber *Callerya* (formerly *Millettia*) *nieuwenhuisii* is colonised by *Cladomyrma andrei* (MASCHWITZ et al. 1989, AGOSTI, MOOG & MASCHWITZ 1999). *Cladomyrma* ant inhabitation has been found in all parts of its distribution. Other ants occasionally nest secondarily in abandoned *Cladomyrma* chambers.

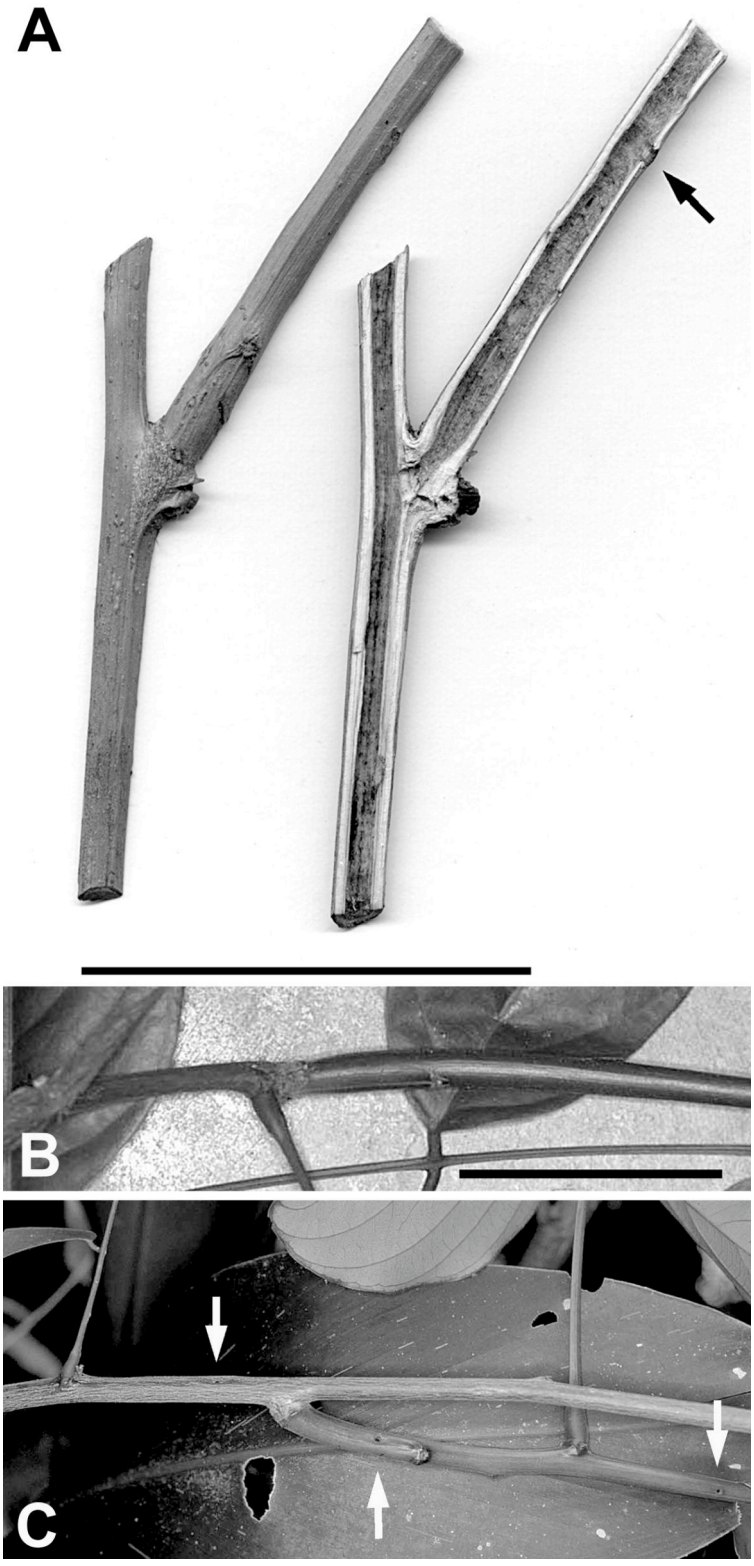


Figure 4-10: Ant-housing structures of *Callerya nieuwenhuisii*. **A**: dissected twig, showing nest chambers hollowed out by *Cladomyrma* ants. Note the increase in diameter in the branching internode; **B**: newly developed swollen internode (domatium) of a young plant; **C**: branching in a mature *Callerya*. The initial increase in diameter slowly decreases with each following internode. Arrows indicate ant entrance holes. Scale bars: 5 cm.

Workers of *Cladomyrma andrei* exhibit a strong preference in their patrolling activity for young developing leaves (Fig. 4-11) and are known to be highly aggressive against stem-destructing entomologists.

Figure 4-11: Young pinnate leaf of *Callerya nieuwenhuisii* patrolled by *Cladomyrma andrei* workers. Arrow indicates entrance hole in stem.

Onset of ant occupation: Generally, liana saplings possess a primary stem diameter too thin to allow ant inhabitation. Thus, colony foundation of *Cladomyrma andrei* usually occurs in swollen domatia which first develop in plants 1 to 1.5 m in length. The minimum internode diameter selected by foundress ants was 4.1 mm (mean 5.6 ± 1.62 SD; n=10). All *Callerya* saplings found in the field (1.1 to 5.5 m; n=11) already harboured *Cladomyrma* ants. With increasing plant and colony size, the entire plant is hollowed out successively and used as nest chamber. For example, a 4.1 m tall *Callerya* provided a total of 6.3 m of stem, branches and twigs of which 6.2 m (98%) were used as nesting space. In another liana (3 m), about 70% of all internodes were colonised by a single colony, the remaining internodes were either solid or harboured colony founding queens.

Ant occupancy rate: All *Callerya nieuwenhuisii* lianas, from saplings to mature plants, found in the field were colonised by *Cladomyrma* ants (100%; n=35). On the canopy walkway in Poring Hot Springs, Sabah, large colonised plants could be found at a height of approx. 30 to 40 m.

Herbarium study: Of the 26 specimens of *C. nieuwenhuisii* examined in several herbaria only 2 (8%) lacked signs of ant occupation and 21 (81%) possessed traits (i.e., hollow stems and entrance holes) pointing to previous *Cladomyrma* colonisation. The remaining 3 (11%), although having hollow stem sections, lacked ant entrance holes, hence the origin of the hollows could not unambiguously be attributed to the efforts of *Cladomyrma* ants. Two collectors mentioned ant symbiosis in the stem: BNB 26475, leg. J. & M.S. CLEMENS, and GEESINK 9243).

Figure 4-12: Woody climber *Callerya nieuwenhuisii* inhabited by *Cladomyrma andrei* (modified from herbarium specimen AMO-008, Lambir Hills NP, Sarawak, leg. U. Maschwitz). Stem hollowed out by ants; arrows indicate entrance holes. Scale bar: 5 cm. Drawing: Jürgen Kisch

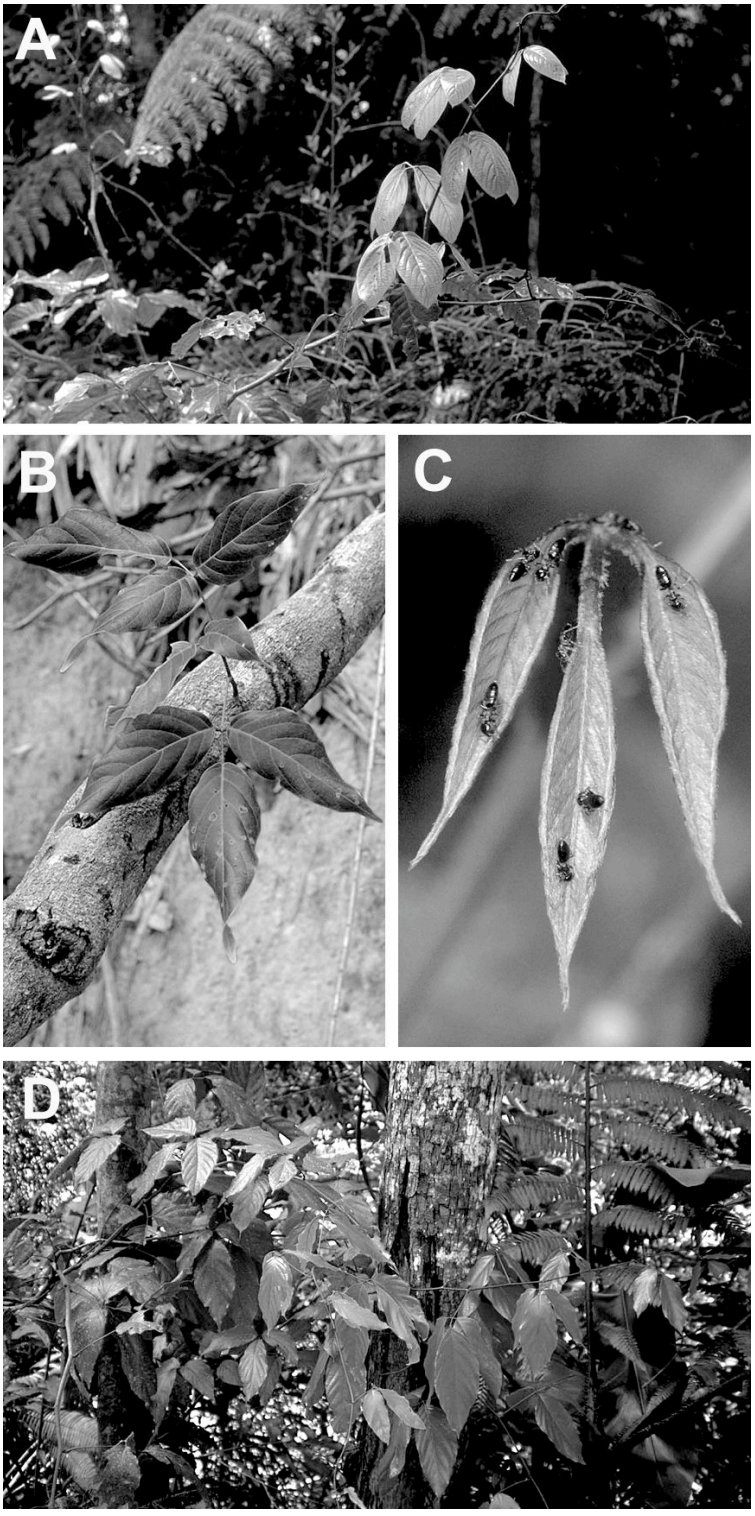


Figure 4-13: *Spatholobus bracteolatus*. **A**: young shoot with red-tinged leaves; **B**: typical trifoliate leaves and stem (8 cm in diameter) of a large plant ca. 35 m long. This section of the plant was abandoned by *Cladomyrma* ants and the interior nest chamber was occupied by *Crematogaster* ants; **C**: workers of *Cladomyrma petalae* patrol a newly developed leaf (centre leaflet 2.5 cm long); **D**: slender plant 9 m long.

Spatholobus bracteolatus Prain ex King

Figures 4-13, 4-14, 4-16, 4-17

Woody climber, up to 30–40 m; locally common; in primary and old secondary forest; from 800 to ca. 1,300–1,400 m altitude (RIDDER-NUMAN & WIRIADINATA 1985, pers. observation). Distribution: West Malaysia (Pahang, Perak, Selangor). A dubious record exists from King's Island (South Myanmar).

Ant-housing structure: Young plants < 5 m produce strongly swollen domatia which usually extend over 2-3 internodes (Fig. 4-14A-C). Compared to the proximal 'normal' internode, the mean increase in diameter of a domatium is 2.6 mm ± 0.83 SD (range 1.5–4.4 mm, n=17).

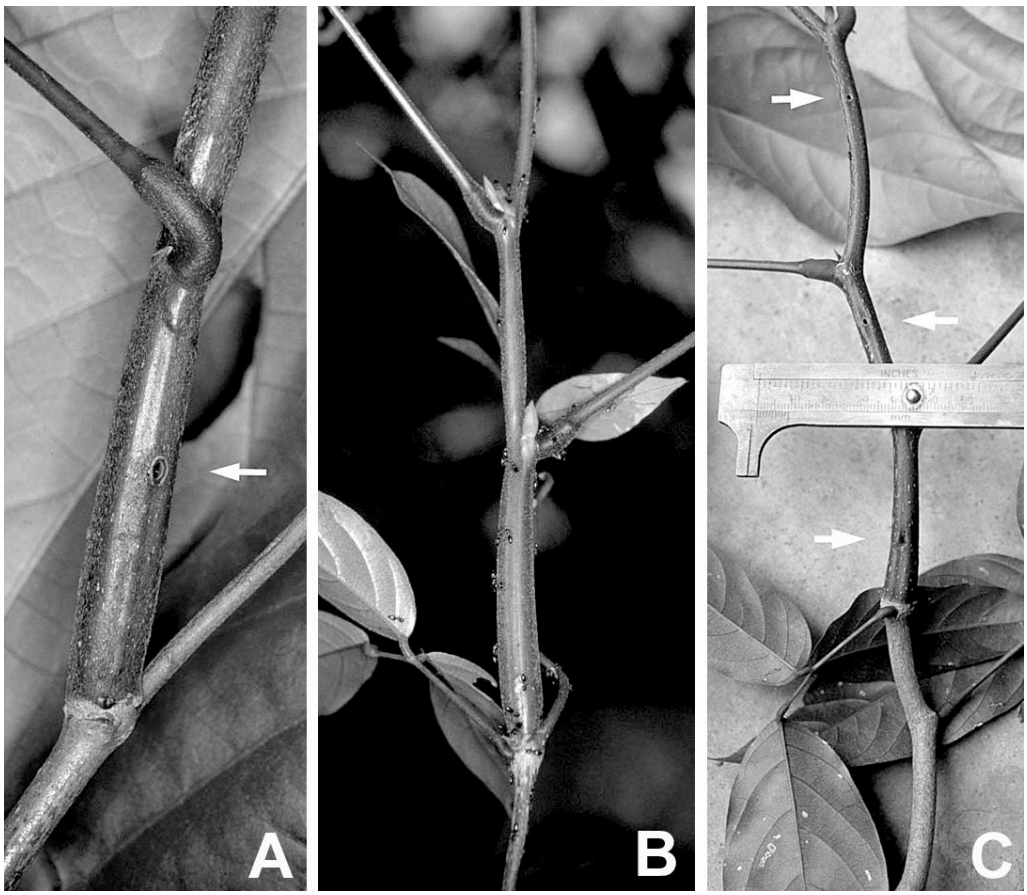


Figure 4-14: Domatia of *Spatholobus bracteolatus*. **A**: swollen internode with entrance hole (arrow); **B**: *Cladomyrma petalae* workers on domatium of young plant (2.4 m long). Note the proximate internode below, which is too small for ant inhabitation; **C**: internodes with entrance holes (arrows). Note the decrease in diameter with each distal internode.

As the plant grows, the increase in diameter of a newly produced domatium relative to the previous internode becomes less pronounced (Fig. 4-14C). In plants > 10 m, the average increase was 0.9 mm ± 0.37 SD (range 0.4–1.6 mm, n=16). However, since a *Spatholobus* plant continuously increases its diameter with each spurt of growth, even the unswollen, 'normal' internodes become more and more suitable for ant inhabitation (see below). The two cuttings of *S. bracteolatus* planted in a greenhouse at Ulu Gombak both produced domatia in the absence of ants.

Ant inhabitants: *Spatholobus bracteolatus* is regularly colonised by *Cladomyrma petalae*, and ant inhabitation has been found in all parts of its distribution. Abandoned *Cladomyrma* founding chambers may occasionally be colonised by various arboreal ants such as species of the genera *Crematogaster Camponotus* and *Technomyrmex*. Rarely, these latter ants succeed in occupying a major portion of the *Cladomyrma* nest system. In three large climbers (20–35m long), whose host trees (phorophytes) were felled due to logging activities, *Crematogaster* ants occupied the main stem whereas the crown was still successfully defended by *Cladomyrma petalae*.

Onset of ant occupancy: The liana is colonised by *Cladomyrma petalae* at an early developmental stage. Saplings produce their first domatia in a height between 0.2 to 1.6 m (n=8). These domatia permit colonisation by colony founding queens, although the primary stem diameter of young lianas is far too small to harbour foundress ants. One plant, 2.4 m in length, already had produced 12 domatia. In young plants, ant occupation is restricted to the domatia, however, later in plant ontogeny, the diameter of the stem is sufficient to allow the ants to excavate nest chambers in 'normal', unswollen internodes (Fig. 4-17). Then, the colony creates a continuous nest system. Inhabitation of twigs by *Cladomyrma* workers requires a pith diameter of at least 1.4 mm (Fig. 4-15). This corresponds to a primary diameter in unswollen 'normal' stems of 3 to 4 mm. Below this threshold, ant colonisation is not possible. Since liana saplings typically have small initial diameters (hence small pith canals), the production of domatia is an important trait to facilitate the colonisation by ants early in the ontogeny of the plant (Fig. 4-16).

Ant occupancy rate: All plants found in the field (n=52), except one, were inhabited by *Cladomyrma* ants, resulting in an occupancy rate of 98%. The single uninhabited plant (1.1 m in length) still lacked a domatium. Size range of occcupied plants was 1.1 to 35 m (mean 10.6 m ± 9.05 SD).

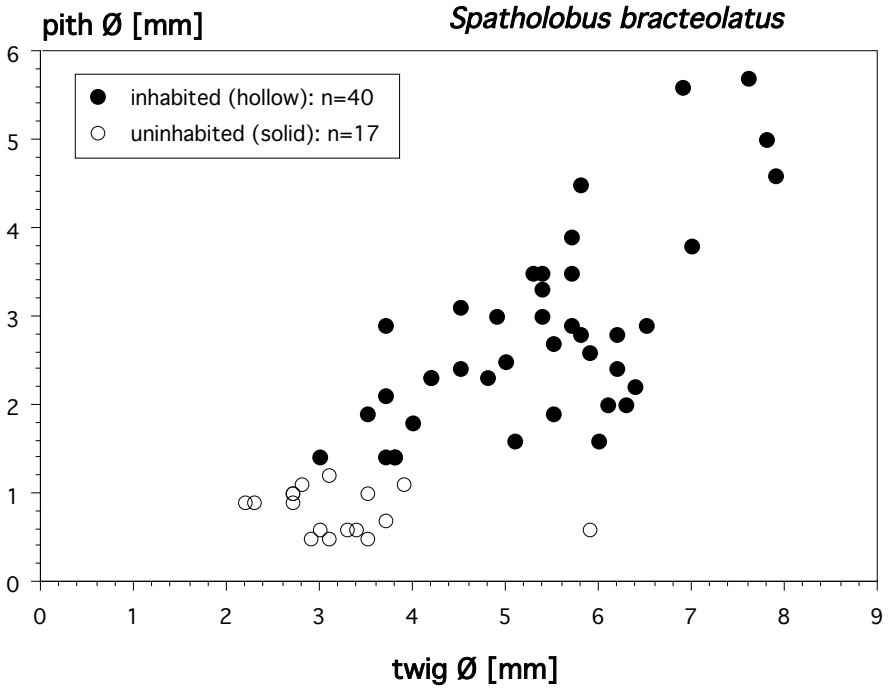


Figure 4-15: Scatterplot of pith and twig diameter of *Spatholobus bracteolatus* in relation to ant occupancy (inhabited versus uninhabited). All measurements were taken from dried herbarium material of both unswollen, 'normal' stem sections and domatia. [Secondary growth is indicated by twig/pith ratios of > 2.]

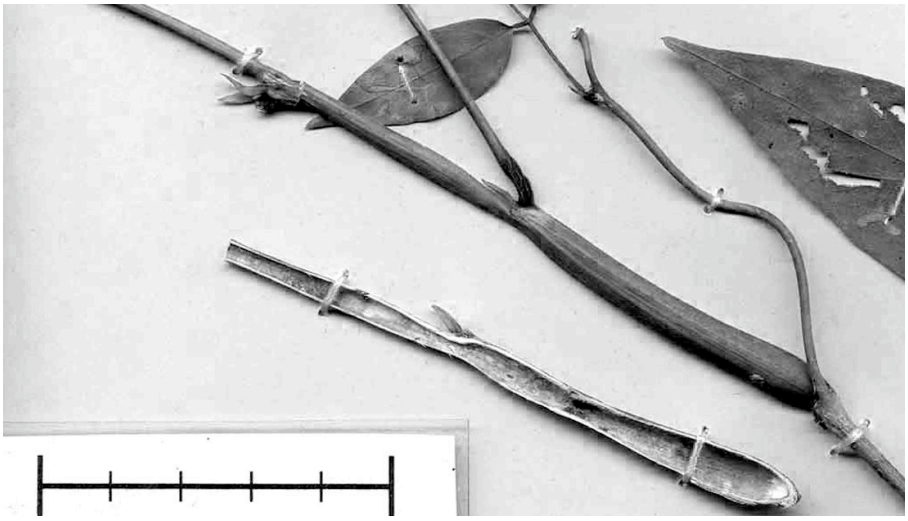


Figure 4-16: Dissected domatium of a young *S. bracteolatus*, 2.4 m in length (dried specimen, AMO-028, leg. J. Moog). Note the spacious domatium. Scale bar: 5 cm.

Herbarium study: *Spatholobus bracteolatus* stands out among most *Spatholobus* species in that it is very rarely collected, although the liana is rather common in some localities (Genting Highlands, Fraser's Hill). Flowering is probably a seldom observed phenomenon (over the years, I could not found a single flowering specimen) and botanists usually avoid collecting sterile specimens. The only available specimen, the type KUNSTLER 8079 (Malay Peninsula, Perak, Gunong Batu Puteh) bears a hollowed out twig with an ant entrance hole typical of *Cladomyrma* origin (size, form, and location along the twig). Another specimen labeled as *S. bracteolatus* I examined at Leiden herbarium, HELFER KD 1825, from King's Island (Mergui Archipelago) off coast Tenasserim (South Myanmar), showed no signs of ant inhabitation, but is most likely not a *bracteolatus*. The specimen was in a poor condition and comparison of vegetative characters with the type specimen was hardly possible.

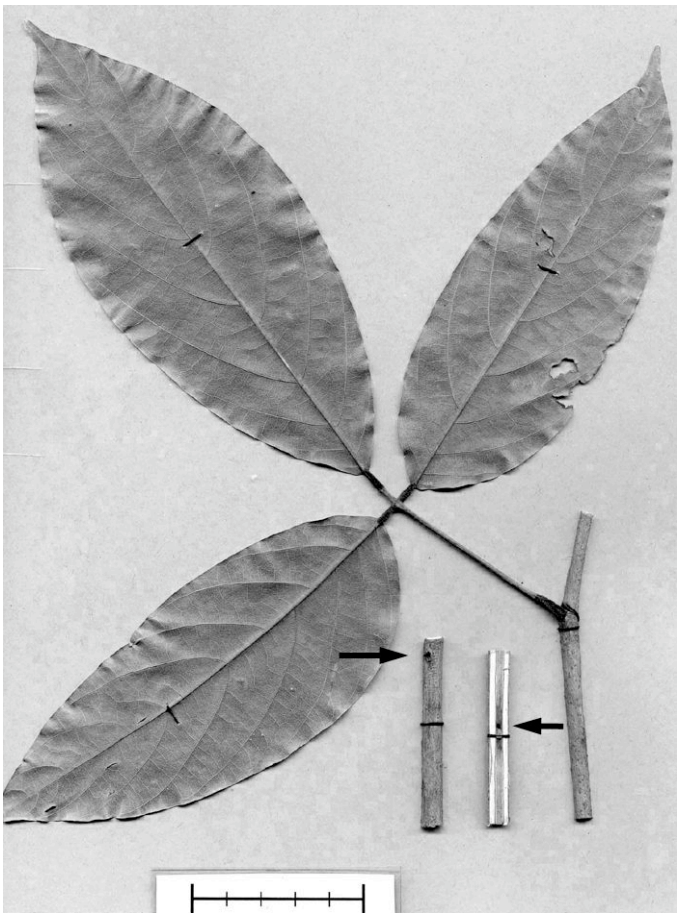


Figure 4-17: Dried specimen of *Spatholobus bracteolatus* (AMO-007; leg. J. Moog). The sheet shows the underside of a typical trifoliolate leaf (with asymmetric lateral leaflets) and short, longitudinally dissected stem sections (unswollen) collected from the crown region. Arrows indicate *Cladomyrma* entrance holes. Scale bar: 5 cm.

Spatholobus oblongifolius Merrill

Figures 4-18, 4-19, 4-20, 4-22, 4-23

Woody climber, up to 30 m; locally common; in primary and old secondary forest, on hill ridges and along rivers; lowlands up to 1,000–1,100 m altitude (RIDDER-NUMAN & WIRIADINATA 1985, pers. observation). Distribution: North Borneo (Brunei, North Kalimantan, Sabah, Sarawak).

Figure 4-18: *Spatholobus oblongifolius*. **A**. trifoliolate leaf, closely resembling those of *S. bracteolatus*; **B**: newly developed, pubescent leaf and young stem with lenticels.

Ant-housing structures: The domatia of *S. oblongifolius* clearly differ from those of *S. bracteolatus*, although the general appearance of the two liana species is very similar. Older plants produce domatia which gradually but distinctly increase their diameter towards the distal node (Fig. 4-19A, C). Young plants (< 3 m) have short internodes with the largest diameter approximately in the centre or upper third of the internode (Fig. 4-19B, Fig. 4-20). In contrast to *S. bracteolatus*, the distension of the domatia in *S. oblongifolius* is less 'bulbous' and does not extend to the following 1 or 2 internodes. Compared to the proximal 'normal' internode, the mean increase in diameter of a domatium is 2.0 mm ± 0.31 SD (range 1.6–2.6 mm, n=11). The pith of swollen internodes is soft and can easily be excavated by the ants. Prostomata are not developed.

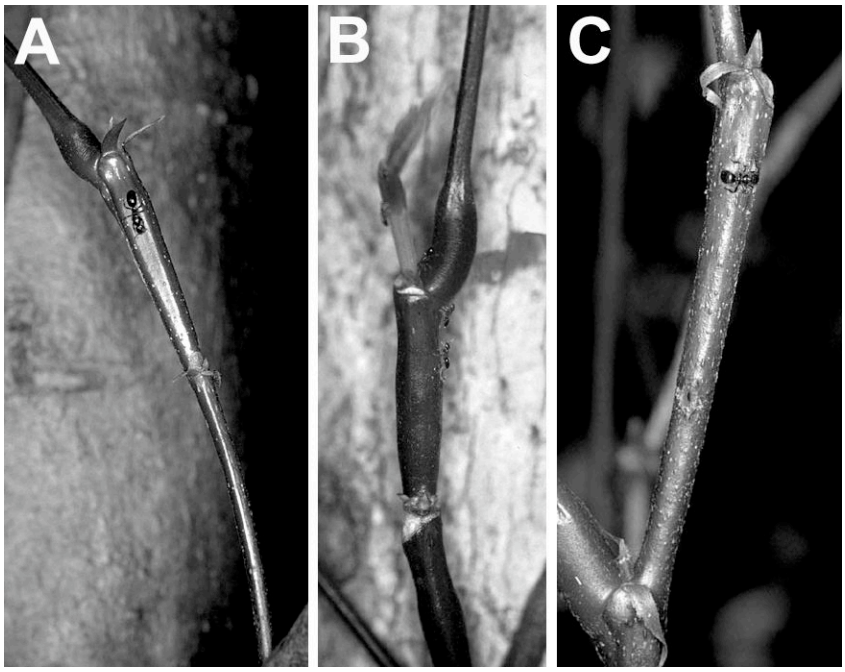


Figure 4-19: Domatia of *Spatholobus oblongifolius*. **A**: new sucker shoot of a plant > 20 m long with the second internode strongly swollen toward the apex. A dealate *Cladomyrma* queen examines the internode for its suitability for colony foundation. After 2.5 h of excavation she entered the internode. On the next day, the foundation chamber had been overtaken by workers of the resident colony; **B**: swollen apex internode of a small plant (0.7 m in length), patrolled by *Cladomyrma* workers; **C**: a dealate *Cladomyrma* queen trying to enter an already occupied foundation chamber but the resident foundress successfully fend her off.

Ant inhabitants: Two *Cladomyrma* species, *C. andrei* and *C. hobbyi*, have been collected from *S. oblongifolius*. Both species also inhabit the tree *Drypetes longifolia*. [A dubious record of *C. maryatiae* is based on the identification of workers only and should be viewed with some caution (AGOSTI, MOOG & MASCHWITZ 1999).] The association of *Cladomyrma* ants with *S. oblongifolius* is known from all parts of its distribution. Founding chambers of *Cladomyrma* may secondarily be occupied by other ant species.

Onset of ant occupancy: The first domatia are produced very early in plant ontogeny. For example, a sapling of 0.4 m length had already developed three domatia of which the first was found at 7.5 cm height and the second at 13 cm.

Another small sapling (total length 0.56 m) also had three domatia, the lowermost placed at 44 cm above the ground (Fig. 4-20). *Cladomyrma* foundress ants colonise these ant-housing structures shortly after their appearance and multiple colonisations of an individual plant are the rule. As in other host plants of *Cladomyrma*, a single colony eventually dominates the host.

Colony founding queens require a minimum domatium diameter of ca. 4 mm (mean 4.9 mm ± 0.656 SD, n=7), which translates into a pith diameter of 2.4 to 3.3 mm. In mature plants, all stems of a suitable size are hollowed out by the ant workers throughout their length. The minimum stem diameter that allows colonisation by *Cladomyrma* workers is 3.8 mm, corresponding to a pith diameter of 1.7 mm (Fig. 4-21). These findings illustrate the importance of domatia for the early establishment of the ant partner.

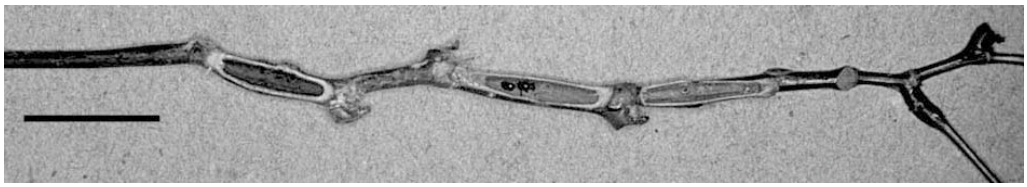


Figure 4-20: Young sapling of *Spatholobus oblongifolius* (0.56 m long) with three domatia, the lowermost (left) at 44 cm height. The three domatia are longitudinally dissected to show the founding chambers of *Cladomyrma*. The domatium in the centre contains a founding queen to illustrate dimensions of founding chamber and foundress ant. Note the abrupt change in diameter from 'normal' internodes to the domatia. Leaves are cut off for more clarity. Scale bar: 2 cm.

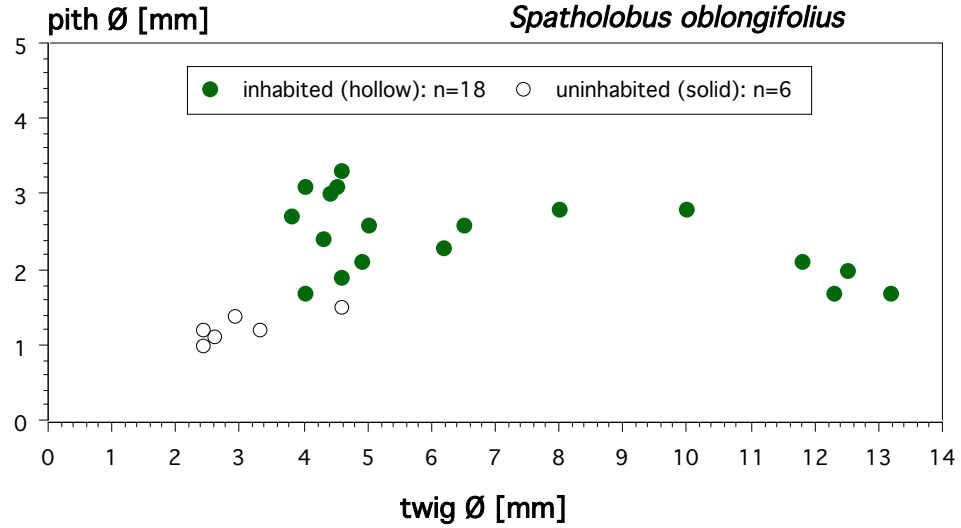


Figure 4-21: Scatterplot of pith and twig diameter of *Spatholobus oblongifolius* in relation to ant occupancy (inhabited versus uninhabited). All measurements were taken from dried herbarium material of both unswollen, 'normal' stem sections and domatia (pithØ > 2.4 mm). [Secondary growth is indicated by twig/pith ratios of > 2.]

Ant occupancy rate: *Spatholobus oblongifolius* is invariably associated with ants. All plants found in the field, either saplings or mature climbers (0.4–28 m; n=44), harboured *Cladomyrma* ants (Fig. 4-22, 4-23).

Figure 4-22: Dried specimen collected from a mature *Spatholobus oblongifolius* climber, >20 m long (AMO-068, leg. J. Moog). The sheet shows new shoots with domatia used for colony foundation and a short section of the main stem axis (lower right), inhabited by the resident *Cladomyrma* colony. Scale bar: 5 cm.

Figure 4-23: Dried specimen of a *Spatholobus oblongifolius* sapling, 0.56 m long (AMO-073, leg. J. Moog). The sheet shows the upper third of the plant, including all three domatia (some leaves removed). Scale bar: 5 cm. [Taxonomic note: in young plants, contrary to the revision (RIDDER-NUMAN & WIRIADINATA 1985), the ultrajugal part of the leaf rhachis can be quite long and thus cannot be used as a character discriminating *S. oblongifolius* from other species. In mature plants, the relative length of the ultrajugal part is 1/6 to 1/19 of the total length of the rhachis (pers. observation).]

Herbarium study: The high occupancy rate (100%) found in the field is also reflected in the herbarium specimens examined (n=41). Traits of ant colonisation were unambiguously observed in 68% of the *S. oblongifolius* specimens (n=28), whereas for 12% of the specimens (n=5) colonisation was unclear (hollow stem sections but no ant holes present). As a rule, *Cladomyrma* ants produce one hole per internode and herbarium specimens may thus seem to lack ant orifices if stem sections collected are too short or if entrance holes face the cardbord onto which the specimen is fixed. Only 8 specimens (20%) lacked any signs of ant occupation. One collector (BNB 26963, leg. J. & M.S. CLEMENS) noticed "symbiosis with ants in the stem."

4.3.3. Loganiaceae

Strychnos vanprukii Craib

Figures 4-24, 4-25, 4-26, 4-27

Slender woody climber, up to 15 m; locally common; in primary and old secondary forest, lowlands up to 1,000–1,100 m altitude [in LEENHOUTS (1962) as *S. quadrangularis* Hill, in LEENHOUTS (1972) corrected to *S. vanprukii*]. Distribution: South and Northeast India, Laos, Vietnam, Thailand, Malay Peninsula (Pahang, Perak, Selangor), and Borneo (Kalimantan, Sarawak).

Figure 4-24: Creeping, shrub-like appearance of *Strychnos vanprukii* in the forest understorey at Ulu Gombak, Selangor, Malay Peninsula.

Ant-housing structures: The stems and twigs apparently do not show any specialised trait related to ant-housing. Neither saplings nor mature climbers provide swollen internodes or thickened nodes (Fig. 4-25, 4-26). However, some internodes become naturally hollow by pith degeneration whereas others on the same plant remain solid. The proportion of naturally hollow internodes within an individual plant varies strongly from 0 to 51% (mean 15.7% ± 13.59 SD, n=14), obviously with a higher proportion in larger plants with larger primary stem diameter. Branches and twigs of a diameter below ca. 4 mm do not become hollow naturally. [Note that bigger-sized branches and twigs do not necessarily become hollow and often remain solid.]

Figure 4-25: Stem of *Strychnos vanprukii*, inhabited by *Cladomyrma petalae* ants. The workers show a preference in their patrolling activity for young developing plant tissue. Stem diameter ca. 5 mm.

Ant inhabitants: In West Malaysia, *Cladomyrma petalae* inhabits *S. vanprukii* in the Ulu Gombak and Ulu Langat region (Selangor). However, *Cladomyrma* inhabitation could not be established for other areas of the plant's distribution. Species of several arboreal ant genera (e.g., *Camponotus*, *Crematogaster*, *Monomorium*, *Tetramorium*) may secondarily occupy preformed chambers created by *Cladomyrma* ants or stemborer larvae.

Onset of ant occupation: As in other host plant species of *Cladomyrma petalae*, a twig suitable for colony-founding queens must have a minimum primary stem diameter of ca. 4 mm, a size that may be reached in plants ≥ 1.5 m long. On average, length of colonised plants was 3.6 m ± 1.95 SD, range 1.5–12.4m, n=35). As mentioned above, many *Strychnos vanprukii* plants provide some naturally hollow internodes due to pith disintegration. Colony-founding *Cladomyrma* queens were found in both previously solid and naturally hollow internodes. Sometimes a solid internode with a hollowed-out foundation chamber was preceded or followed by a naturally hollow internode, indicating that the founding queens do not discriminate between the two internode types.

Surprisingly, the plants were never occupied throughout their length, a finding contrasting sharply to the nest structure observed in most other host plants of *C. petalae*. Measurements of the plant proportion inhabited showed that at most 39% of the available internodes were occupied by *Cladomyrma* (mean 8.7% ± 9.32 SD, median 4.8%, n=16). Correspondingly, colony size was usually small and did not exceed 600 workers. Alate sexuals of *C. petalae* in *Strychnos vanprukii* have never been found.

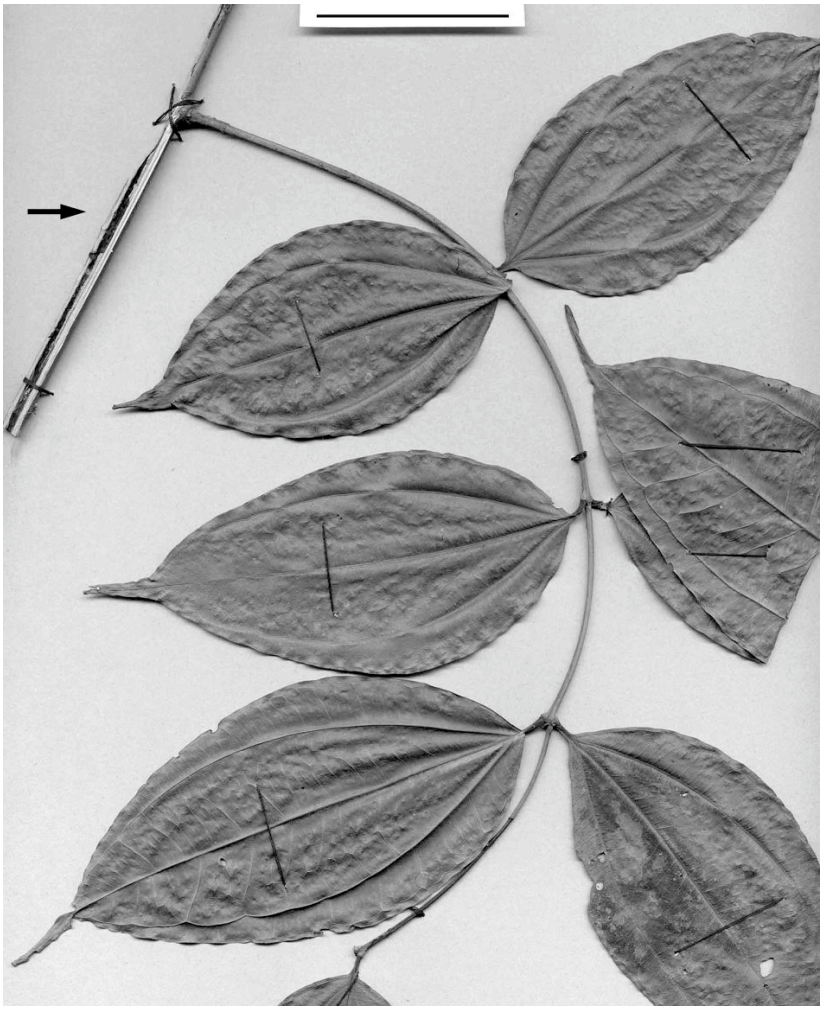


Figure 4-26: Dried specimen of *Strychnos vanprukii*, a climber 3.5 m long (AMO-012, Ulu Gombak, Malay Peninsula, leg. J. Moog). Arrow indicates hollowed-out stem used as nesting space by *Cladomyrma petalae* ants. Scale bar: 5 cm.

Ant occupancy rate: Of 101 *Strychnos vanprukii* plants found in the study area (0.65 to 12.4 m in length) only 35% were colonised by *Cladomyrma* ants. Of these, more than half (19) harboured a single colony founding queen not yet having produced workers. If only colonies are considered, occupancy rate is even lower (16%).

Herbarium study: The examination of 16 herbarium specimens of *Strychnos vanprukii* from India (n=3), Laos (n=1), Vietnam (n=2), Thailand (n=2), Malay Peninsula (n=6), and Borneo (n=2) yielded a single specimen with signs of previous *Cladomyrma* occupancy (VAN MEER 1890) from the Ulu Langat Forest Reserve, a region close to my main study area at Ulu Gombak. It should be noted, however, that the Malayan material differs in vegetative characters from the remaining material collected in Continental Asia and Borneo by generally having larger leaves and

rounded (not sharply) quadrangular young twigs (Fig. 4-25, 4-26). Since the flowers of Malayan *S. vanprukii*, (formerly treated as *S. quadrangularis*) are inadequately known (LEENHOUTS 1967), it remains to be shown whether these differences in vegetative characters are of an intra- or interspecific nature.

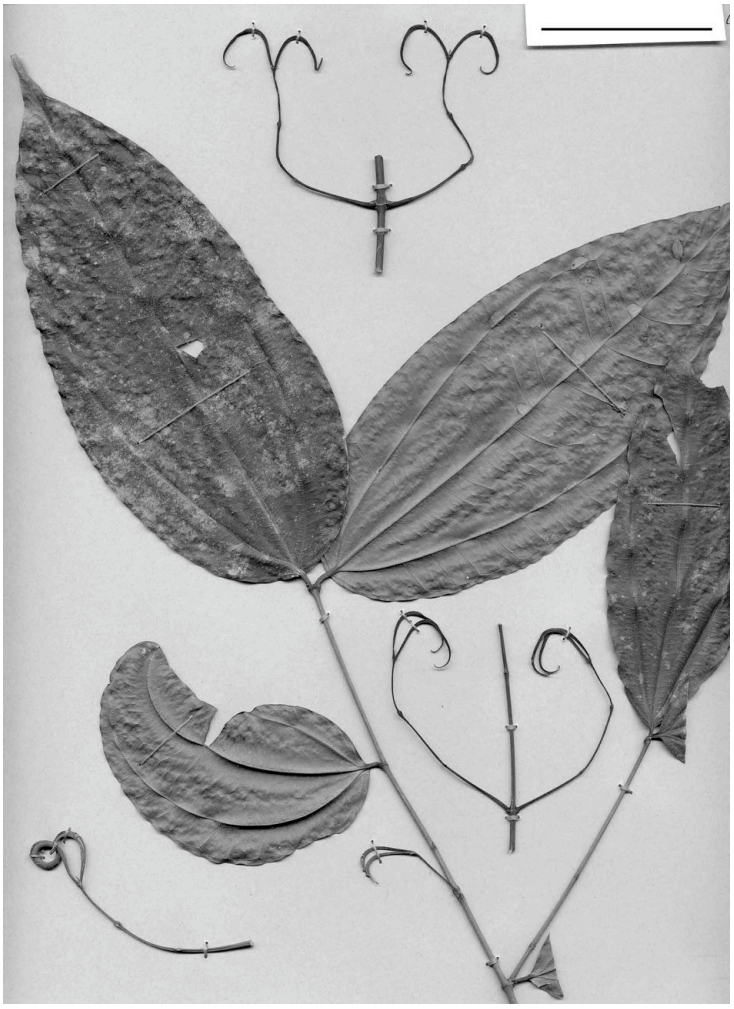


Figure 4-27: Dried specimen of *Strychnos vanprukii*, 3.9 m in length (AMO-020, Ulu Gombak, Malay Peninsula, leg. J. Moog). Note the characteristic paired, hooked tendrils. Scale bar: 5 cm.

4.3.4. Rutaceae

***Luvunga* sp.** Buch.-Ham.

Figures 4-28, 4-29, 4-30, 4-31

Slender woody climber, up to ca. 15 m; rare; in primary and old secondary forest, 300 to 900 m altitude (pers. observation). Distribution: Malay Peninsula (Pahang, Perak, Selangor). Note: This plant could not be identified to species level. *Luvunga* is a well-characterised, readily recognisable genus (SWINGLE 1967), but species delimitation within the genus is poorly understood (STONE 1985), and identification of sterile collections is extremely difficult (D. T. JONES, pers. comm.). Furthermore, the *Luvunga* specimens I have examined at several herbaria often bore none or contradicting identification labels. A critical review of the genus is needed.

Figure 4-28: *Luvunga* sp. treelet, 1.75 m tall. The climbing habit of this species is visible only after the plant reaches a height of about 2 meters.

Ant-housing structures: Young plants produce swollen internodes which gradually increase their diameter towards the node (Fig. 4-29). The increase in outer diameter of a domatium varies between 1.2 to 2.0 mm (mean 1.5 mm ± 0.29 SD, n=10). Plants develop their first domatia in heights between 0.2 to 0.8 m (mean 0.4 ± 0.16 SD, n=13). Prostomata are absent and the soft pith must be excavated by colonising ants to create a cavity.

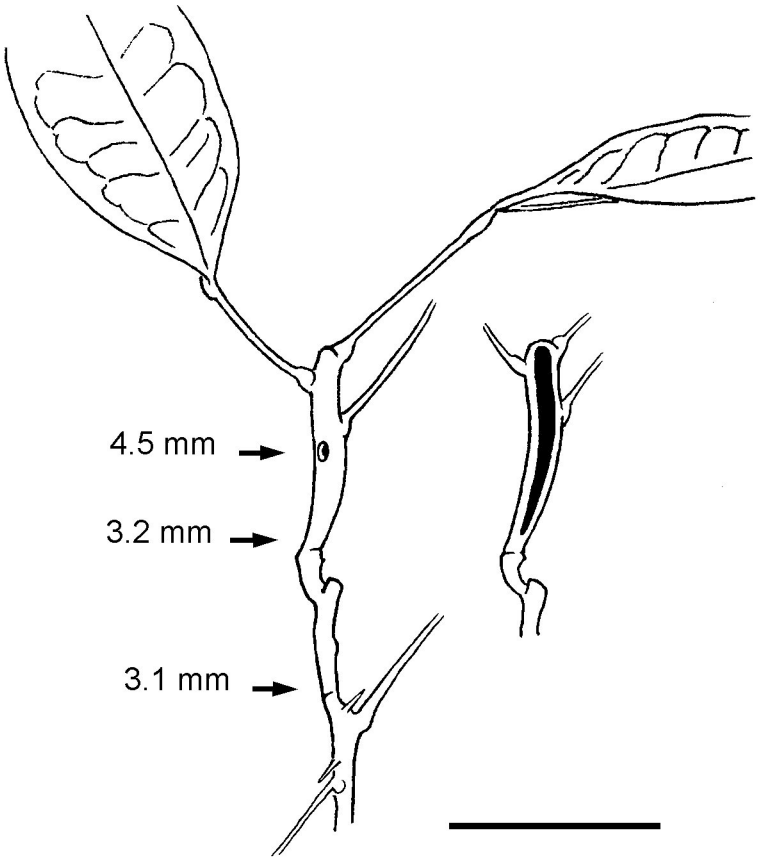


Figure 4-29: Domatium at the apex of a young *Luvunga* sp. (0.8 m in height) inhabited by a young *Cladomyrma* colony consisting of a queen and 8 workers. The internodes are swollen towards the node. Given are outer diameters of the internodes at different locations along the stem. The inset, right, shows the longitudinally split domatium with the ant's nest chamber. Three additional domatia (not shown), containing dead founding queens, had been produced by the plant at heights of 56, 60 and 63 cm. Scale bar: 3 cm. Drawing: J. Moog.

Ant inhabitants: *Cladomyrma petalae* regularly colonises this *Luvunga* species in the Main Range of the Malay Peninsula. Several *Crematogaster* species and other arboreal ants may secondarily inhabit the nest chambers hollowed-out by *Cladomyrma* ants.

Onset of ant occupation: Colony initiation of *Cladomyrma* starts immediately after the development of the first domatia. Founding queens were collected from domatia of small saplings at heights of only 20 to 50 cm. Multiple colonisations of an individual *Luvunga* are the rule but, eventually, a single colony dominates the host and most of the plant's stems are used as nest chamber (Fig. 4-31).

Figure 4-30: *Luvunga* sp. with trifoliolate and unifoliolate leaves as well as stem sections hollowed out by *Cladomyrma* ants (left: AMO-051, 4.5 m long; right: AMO-050, 1.9 m long). Trifoliolate leaves begin to develop in plants > 2 m. *Luvunga* climbers cling to forest trees by means of recurved spines in the axils of leaves. In younger plants (right), the spines are still straight and the plant has the appearance of a treelet. Scale bar: 5 cm. Drawing: Jürgen Kisch.

Ant occupancy rate: A total of 35 *Luvunga* plants were found in the field (mean length 1.3 m ± 1.44 SD, range 0.22 to 8.0 m). Percentage of colonisation was high, with 86% overall (n=30) and 100% for plants > 0.75 m (n=20).

Herbarium study: The examination of herbarium material yielded confusing results. Several differently labeled *Luvunga* collections, i.e., *L. crassifolia* Tan., *L. sarmentosa* (Bl.) Kurz, *L. scandens* (Roxb.) Buch.-Ham. and *L.* sp., contained a specimen each with hollow twigs and entrance holes strongly indicating previous *Cladomyrma* occupation. However, these myrmecophytic specimens (FRI 1578, FRI 2552, FRI 23154 and SCORTECHINI 624) all appeared to belong to a single (new?) species. In vegetative characters these specimens matched the older plants I collected in the field

(Fig. 4-30, 4-31). Additionally, many species folders in the herbaria were mixed. A critical study of the genus is needed badly.

Figure 4-31: Dried specimen of *Luvunga* sp. climber, 8 m long (AMO-055, Fraser's Hill, Malay Peninsula, leg. J. Moog). The longitudinally dissected stem sections show the nest chamber of *Cladomyrma*. Note that leaf type and shape as well as spine form change with plant ontogeny (compare Fig. 4-28 and 4-30). Scale bar: 5 cm.

4.3.5. Achariaceae

Ryparosa fasciculata King

Figures 4-32, 4-33, 4-35

Tree, up to 20 m; uncommon; in primary and old secondary forest, lowlands to 900 m altitude (SLEUMER 1954, pers. observation). Distribution: Malay Peninsula. Note: The genus has been traditionally assigned to the Flacourtiaceae but is now transferred to the Achariaceae (CHASE et al. 2002).

Figure 4-32: *Ryparosa fasciculata*, sucker shoot of fallen tree (3.6 m long). The petioles of the leaves are swollen at both ends, often curved at the apex. Cutting the bark produces a distinct cyanide smell.

Figure 4-33: Young shoots of *Ryparosa fasciculata* with the typical numerous linear-oblong lenticels. The nodes are slightly thickened and the primary diameter of young branchlets is usually increased towards the apex.

Ant-housing structures: The branchlets are slightly thickened at the nodes (Fig. 4-33) which support the large leaves (up to 55 cm). Although there is no obvious swelling of the twigs, the primary twig diameter of small saplings between 0.4 to 1 m in height is usually large enough to allow the colonisation by colony founding *Cladomyrma* ants which excavate the pith. The hollowed-out pith canal is large, representing a space 2.0 to 3.9 mm across.

Ant inhabitants: Two *Cladomyrma* ant species, namely the rare *C. nudidorsalis* and the common *C. petalae*, regularly inhabit *R. fasciculata* (MOOG et al. 1997, AGOSTI, MOOG & MASCHWITZ 1999). The association with *Cladomyrma* ants is known from all parts of West Malaysia.

Onset of ant occupation: Colony-founding *Cladomyrma* queens were already observed in three saplings 0.35–0.4 m tall. All plants above 1.4 m in height harboured *Cladomyrma* ants. The smallest diameter of a twig harbouring a *Cladomyrma* foundress was 4.4 mm (mean 5.9 ± 1.35 SD, n=15). The nest structure of a small tree (1.15 m tall) dissected in its entirety is presented in Fig. 4-34. Here, the first but unsuccessful attempt to initiate a colony was found at approx. 0.5 m height (base of branch A). The nest chamber of one branch (D) was secondarily colonised by a myrmicine ant species. In sum, 37% of the wood (84 of 233 cm) was hollowed out by *Cladomyrma* ants. As in other *Cladomyrma* host plants, the proportion of a plant's total wood excavated as nest chamber increases with plant size or age (Tab. 4-2).

Ant occupancy rate: Fortyseven plants were found in the field (mean tree height 3.5 m ± 2.89 SD, range 0.35–16 m), of which 91.5% (n=43) were inhabited either by *Cladomyrma nudidorsalis* or *C. petalae*. Occupancy rate reached 100% for plants > 1.4 m in height (n=34). However, because the sample size of adult plants was low in this study, it is not yet known whether the observed occupancy rate is maintained in mature reproductive trees.

Colony size and associated trophobionts: Colony size varied strongly according to plant size or portion of the plant occupied (Tab. 4-2). Established colonies of *Cladomyrma* reached a size of approximately 3000–5000 workers in trees greater than 5 m in height. A small sample of trophobionts collected from *R. fasciculata* stems have been so far identified as belonging to the Pseudococcidae [*Crenicoccus cladomyrmae* Williams, *Crenicoccus gullanae* Williams, *Maconellicoccus multipori* (Takahashi), and *Pseudococcus aurantiacus* Williams; WILLIAMS 2004], and to the Coccidae [*Coccus macarangae* Morrison and *Coccus* secretus (Morrison); HECKROTH et al., 1998]. These coccoids –as in other *Cladomyrma* systems– were always

restricted to the stem interior and were never observed to be tended by *Cladomyrma* on the outer surface of the host plants. The ratio of coccoids to worker ants was variable (Tab. 4-2), ranging from 1 : 5 to 1 : 13 (mean 1 : 9; n = 9), but may be dependent on factors such as the ontogeny of the ant colony, the identity of associated coccoid taxa, nymphal stages of the coccoids, or unquantified environmental variables within the study populations of *R. fasciculata*.

tree height (cm)	queens (n)	workers (n)	stem holes (n)	excavated stem (%)	colony coccoids (n)
35	1[1]	75	5	–	8
52	1	340	7	–	34
115	1[2]	134	12	37	27
235	1	1100	41	66	143
240	1	~2000	48	–	188
290	1	~500	–	46	–
350	1[3]	759	31	85	92
550	1[4]	860	29	–	85
580	1	3760	–	–	287
650	1[5]	245	5	–	30

Table 4-2: Tree height, queen number, ant colony size, entrance holes, proportion of the total wood excavated as nest and associated hemipteran trophobionts for *Ryparosa fasciculata* individuals colonised by *Cladomyrma* (examples).
Note: [1] the plant also contained five founding queens in separate chambers, of which four were dead (probably killed by the incipient colony); [2] a small hollow twig was occupied by myrmicine ants that inhabited an abandoned *Cladomyrma* chamber; a founding chamber of *Cladomyrma* was empty; [3] female alates were found; [4] only the crown was colonised; the bole was not hollowed; [5] the colony occupied only a side shoot of the crown. Crown and bole were hollowed out but the former occupant *Cladomyrma* colony had died.

Food rewards: The spatial distribution of *Cladomyrma* workers on the surfaces of *R. fasciculata* was significantly biased towards young, immature plant parts. I was unable to find any evidence that this concentration of ant activity on young shoots and leaves was coupled with the provisioning of food rewards, such as food bodies (FBs) or extrafloral nectar (see chapter 8, p. 215). On no occasions were *Cladomyrma* workers observed harvesting FBs, although several *Ryparosa* species are known to produce such plant structures (WEBBER, ABALOZ & WOODROW 2007). FB scars, however, were observed on the young stems and abaxial leaf surfaces of some herbarium specimens of *R. fasciculata* (WEBBER et al. 2007). Interestingly, all ant-inhabited *Ryparosa* species had the lowest proportion of specimens with conclusive evidence of FB scars.

This may suggest that FB production is decreased in these species, perhaps in response to food sources provided by hemipteran trophobionts.

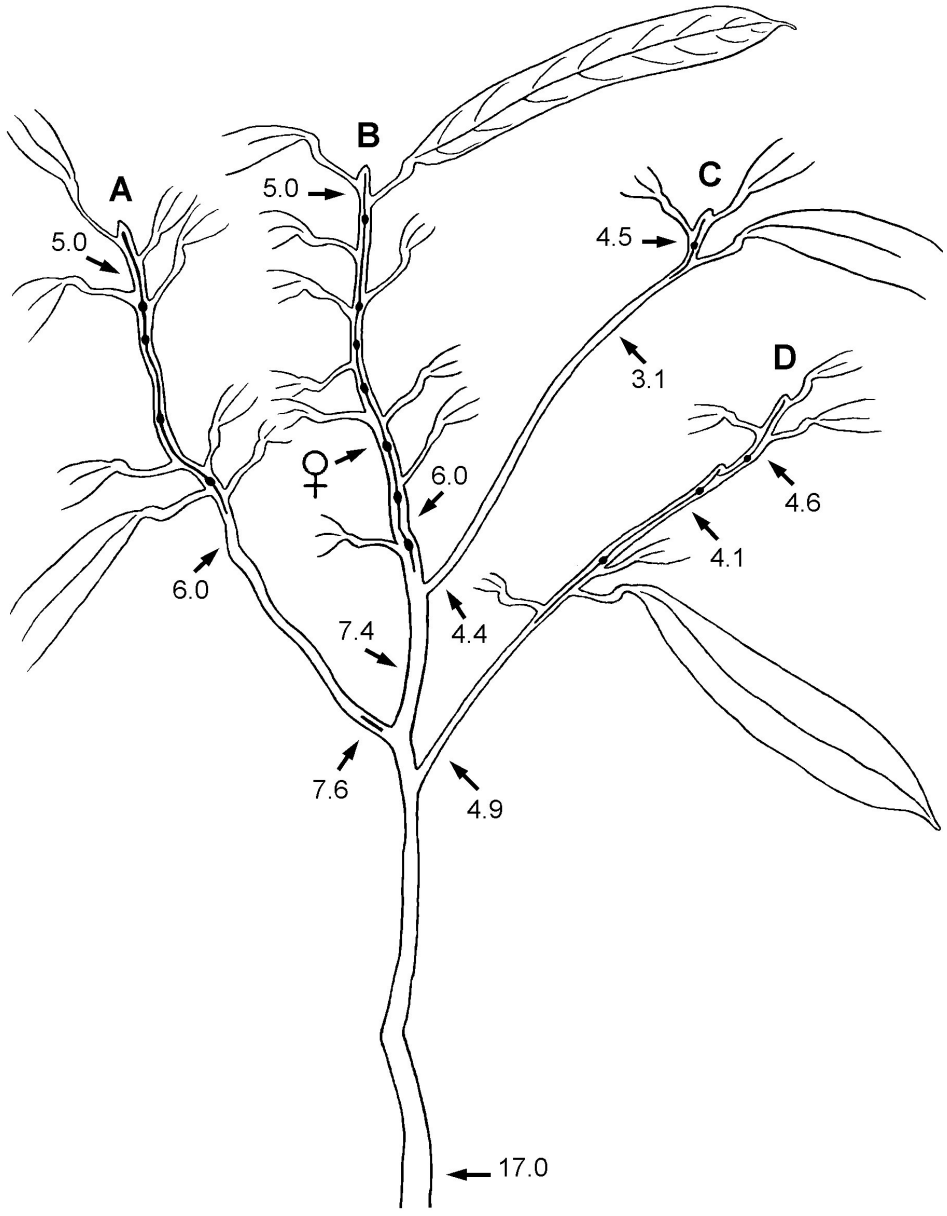


Figure 4-34: Distribution of *Cladomyrma* nest chambers in a juvenile *Ryparosa fasciculata*, 1.15 m in height. In total, the colony contained 134 workers and 27 coccoids. The female symbol is where the physogastric colony queen was found. Stem diameters are given in mm. Solid black circles indicate the 15 entrance holes (for more clarity all facing the observer). The basal cavity of branch A originated from a previous, unsuccessful colony foundation. The *Cladomyrma* nest chamber of branch D is secondarily occupied by a small myrmicine colony. Note that stem diameter at apex of branch C and D is increased compared to mid-branch diameters. In total, 37% of the wood was hollowed out by *Cladomyrma* ants. Drawing: J. Moog.

Figure 4-35: Dried specimen of a *Ryparosa fasciculata*, 3.6 m in height (AMO-029, Fraser's Hill, Malay Peninsula, leg. J. Moog). Dissected stem sections show nest chambers of *Cladomyrma petalae* ants. Overall, 85% of the plant's wood was hollowed out by the ants and used as nest chamber. Arrows indicate entrance holes. Scale bar: 5 cm.

Herbarium study: The regular ant occupation observed in the field is mirrored by the results obtained from the examination of herbarium specimens. In 80% of the collections assigned to *R. fasciculata* (n=15), the twigs were hollow and possessed the typical entrance holes of *Cladomyrma* (Fig. 4-35). One specimen (YL 6729, leg. Y. LAUMONIER) from Sumatra is apparently a misidentification. None of the collectors mentioned ant inhabitation of the stem.

Ryparosa porcata P.F. Stevens

Figures 4-36, 4-37A

Tree, up to 18 m; uncommon; in primary and old secondary forest, or in forest over limestone; 100–150 m altitude (JARVIE & STEVENS 1998). Distribution: Borneo (Central Kalimantan, Sarawak). Note: Species not found in the field.

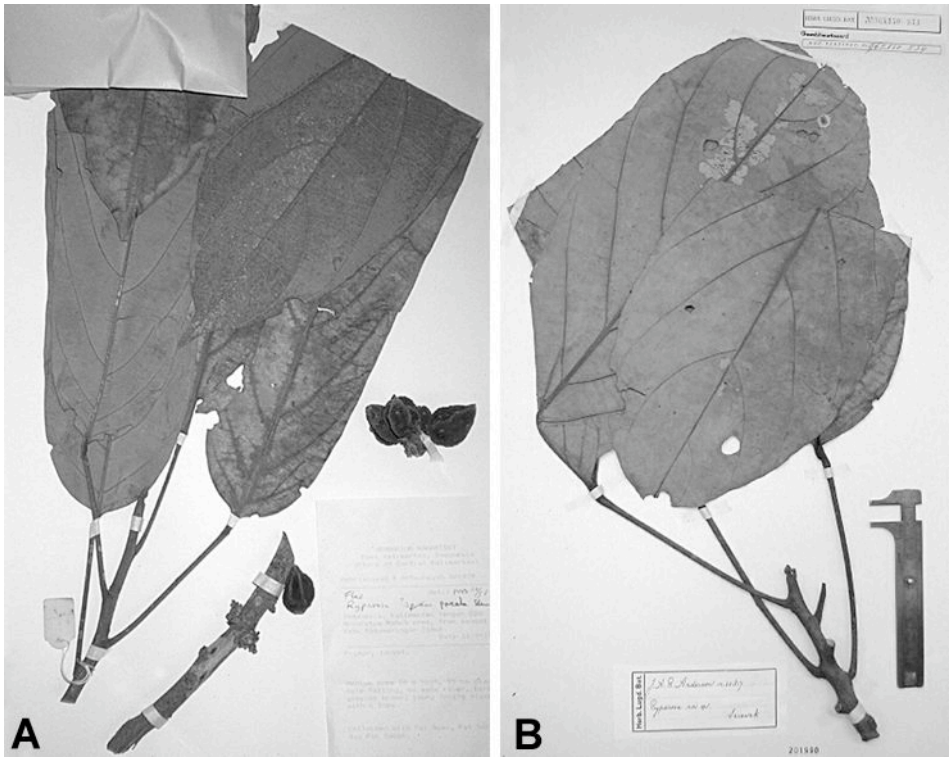


Figure 4-36: Dried specimens of *Ryparosa porcata* examined at Leiden herbarium. **A**: AA 1979, Central Kalimantan, Borneo, leg. Ambrainsyah & Arbainsyah; **B**: S.20817, Serian district, Sarawak, Borneo, leg. J. A. R. Anderson. In vegetative characters, *R. porcata* differs from *R. fasciculata* by having less narrow leaves, more secondary veins and distinctly longer petioles. Scale: calliper rule set to 1 cm.

Ant inhabitants: *Ryparosa porcata*, a newly described species from Borneo, has been reported to be inhabited by unidentified ants (JARVIE & STEVENS 1998). The two available herbarium specimens checked at Leiden herbarium (AA 1979 and S.20817) showed signs of ant occupation typical for *Cladomyrma*. And indeed, the remains of ant workers collected out of one specimen (AA 1979) could be identified with certainty as belonging to the genus *Cladomyrma*. It was, however, not possible to identify the worker corpses to species level. According to the herbar collections, the ant-housing

structures appear to be very similar to *R. fasciculata* (Fig. 4-37A). Onset of ant occupation and occupancy rate is not known.

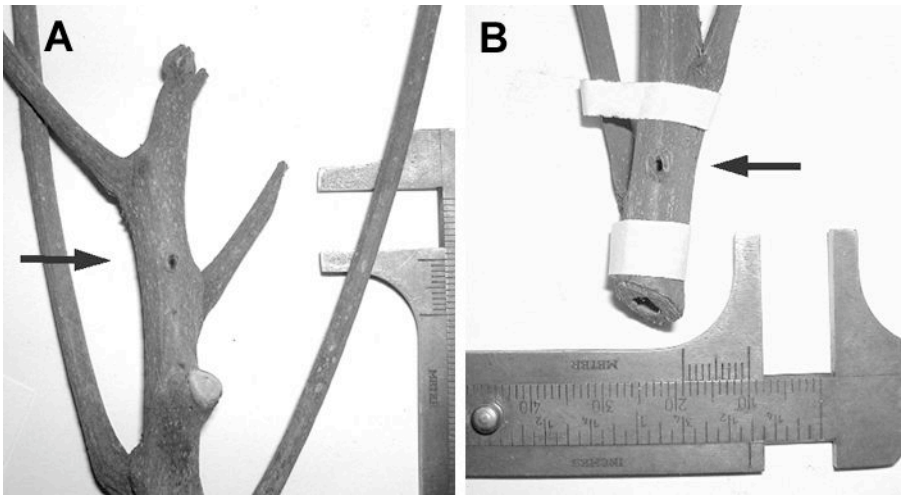


Figure 4-37: Stem sections of *Ryparosa* specimens with ant entrance holes (arrows). **A**: *Ryparosa porcata*, S.20817, Serian district, Sarawak, Borneo, leg. J. A. R: Anderson; **B**: *Ryparosa* sp. nov. aff. *calotricha*, Burley et al. 686, Central Kalimantan, Borneo, leg. J. S. Burley et al. Scale: calliper rule 1 cm.

Herbarium study: All three collections (CHURCH 892, AA 1979, and S.20817) assigned by JARVIE & STEVENS (1998) to the new species *Ryparosa porcata* are reported to have hollow pith and exit holes along the twigs, suggesting that this plant is associated with ants, although this was not noted by any of the collectors. Two of these specimens were available to me and I could verify the assumption of myrmecophily and even found *Cladomyrma* remains inside the twigs of collection AA 1979.

Ryparosa* sp. nov. aff. *calotricha

Figure 4-37B

The specimen BURLEY et al. 686, labeled as "*Ryparosa* sp. nov., cf. S.20817" at Leiden herbarium also showed entrance holes typical of *Cladomyrma* (Fig. 4-37B). It differs in sterile features such as leaf venation and leaf shape from other *Ryparosa* collections. The specimen belongs to a poorly known taxon from Borneo (Kalimantan, Sarawak) not yet formally described and most probably represents a new species (*R.* sp. nov. aff. *calotricha*, sensu WEBBER & WOODROW 2006). Of the four collections of which I am aware, three had excavated stems and ant entry holes (WEBBER et al. 2007b). Stem swellings were not present in any of these specimens.

Ryparosa anterides B.L. Webber

Other collections from East Borneo have recently been described as the new species *R. anterides* (WEBBER & WOODROW 2006). The tree is consistently taller (25–40 m) than any other known *Ryparosa* species and has prominent buttressing. It is known only from the rainforests of east Kalimantan, sometimes on sand or loam soil containing limestone rocks and in wet or periodically inundated areas, at 10–400 m altitude; noted as uncommon to rare by KOSTERMANS in the 1950s. The majority of *R. anterides* herbarium specimens (13 of 18) had typical entrance holes in excavated stems and/or prominent shoot tip swellings (e.g. KOSTERMANS 13440 and 21216), the taxon is thus likely a host of *Cladomyrma* ants (WEBBER et al. 2007b).

[***Ryparosa amplifolia*** (K. Sch.) Mildbr.]

This New Guinean species has been frequently reported to have associations with ants, making it necessary to examine its potential as host of *Cladomyrma* (although the ant genus is not yet known to occur east of Borneo). SCHUMANN & LAUTERBACH (1901) mentioned swollen shoot tips, hollow stems and the presence of undetermined ants in *Gertrudia amplifolia* K. Sch. [syn. *R. javanica* (Blume) Kurz ex Koord. & Valeton sensu SLEUMER 1954]. A number of current reviews still refer to the original synonym, creating some confusion (e.g., HÖLLDOBLER & WILSON 1990; JOLIVET 1996). Recently, WEBBER & WOODROW (2006) cleared up the taxonomic mess of the *Ryparosa javanica* species complex and reinstated the taxon.

Ryparosa amplifolia is a tree 14–22(–30) m tall, growing in rainforest habitats up to 300 m, occasionally much higher, and is often found near rivers and streams. Examination of herbarium material revealed that the majority of specimens (29 of 51) had evidence of ant occupation (WEBBER et al. 2007, own observations). Associated with the swollen shoot apices were elongated, slit-like prostomata (up to 15 mm in length), the favoured sites for multiple entrance holes (c. 5 mm apart). However, the size and distribution of entry holes were irregular between specimens, indicating that they were most probably caused by ant species different from *Cladomyrma*. Furthermore, a *Camponotus* (probably *rubiginosus* species group) worker was found in one specimen (Neth. Ind. For. Serv., bb25751, WEBBER et al. 2007).

4.3.6. Crypteroniaceae

Crypteronia griffithii Clarke in Hook. f.

Figures 4-38, 4-39, 4-40, 4-46

Tree, occasionally up to 40 m; uncommon to locally common; in primary forest and old secondary forest; lowlands to 750 m altitude (BEUSEKOM-OSINGA 1977, PEREIRA 1996, pers. observation). Distribution: South Myanmar (1 collection), throughout the Malay Peninsula and Borneo, Central Sumatra (Jambi).

Figure 4-38: *Crypteronia griffithii*. **A**: tree, ca. 5 m in height, at steep slope with crown at level of ridge top; **B**: sapling, 1.4 m tall, with young leaf herbivory at twig not yet inhabited by *Cladomyrma* ants; **C**: twig of healthy treelet, 2.6 m tall, inhabited by *Cladomyrma* ants.

Ant-housing structures: The twigs are swollen at the nodes (Fig. 4-39A-B). On average, the primary diameter increased from mid-internode to the node (measured at the attachment of the petioles) by about 3.5 mm (n=20). In young shoots, the pith canal (which is the more important trait with respect to ant inhabitation) increased by 1.24 mm ± 0.39 SD, n=73). Prostomata are not developed (MOOG, DRUDE & MASCHWITZ 1998).

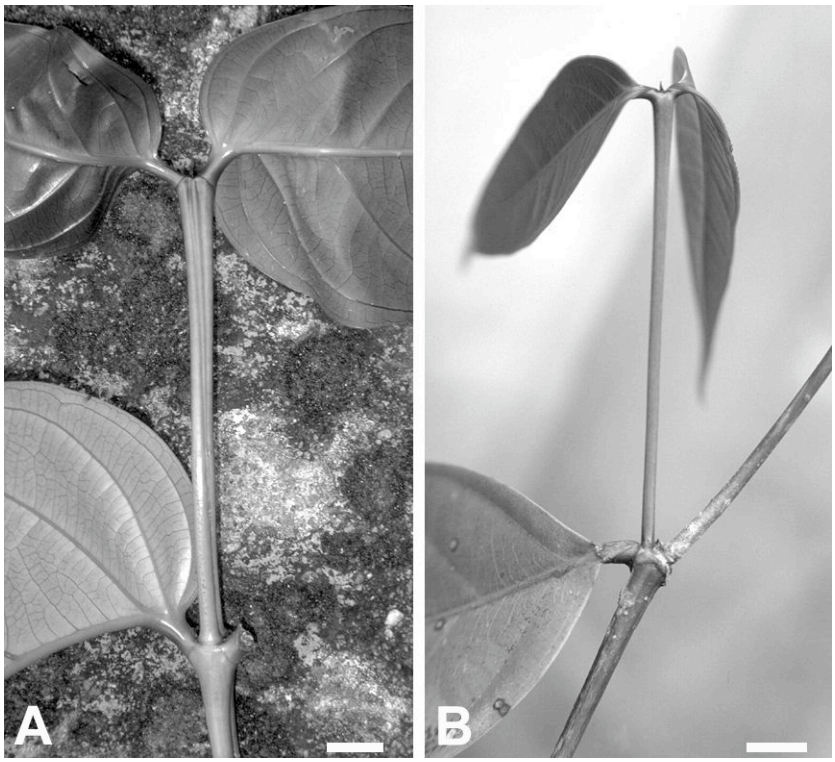


Figure 4-39: Young twigs of *Crypteronia griffithii* with swollen nodes. **A**: shoot with blue-purplish leaves of a tree ca. 4 m in height (Sumatra); **B**: shoot of a sapling 0.8 m tall (Malay Peninsula). Scale bar: 1 cm.

Ant inhabitants: *Crypteronia griffithii* is occupied by two *Cladomyrma* species, *C. crypteroniae* and *C. maschwitzi*. Whereas the latter occupies the host in all parts of its distribution (Borneo, Malay Peninsula and Central Sumatra), the former is absent from the Malay Peninsula. A detailed account of the association between the host and *C. maschwitzi* is given in MOOG, DRUDE & MASCHWITZ (1998).

Onset of ant occupation: The tree is colonised by *Cladomyrma maschwitzi* at an early developmental stage. Colonisation starts in saplings between 0.5 to 0.8 m in height. Founding queens of *C. maschwitzi* always colonise young twigs close to the swollen node (Fig. 4-40) and they require a minimum outer diameter of 3 mm (mean 4.2 ± 0.69 SD; range 3.0–5.8 mm; n=71).

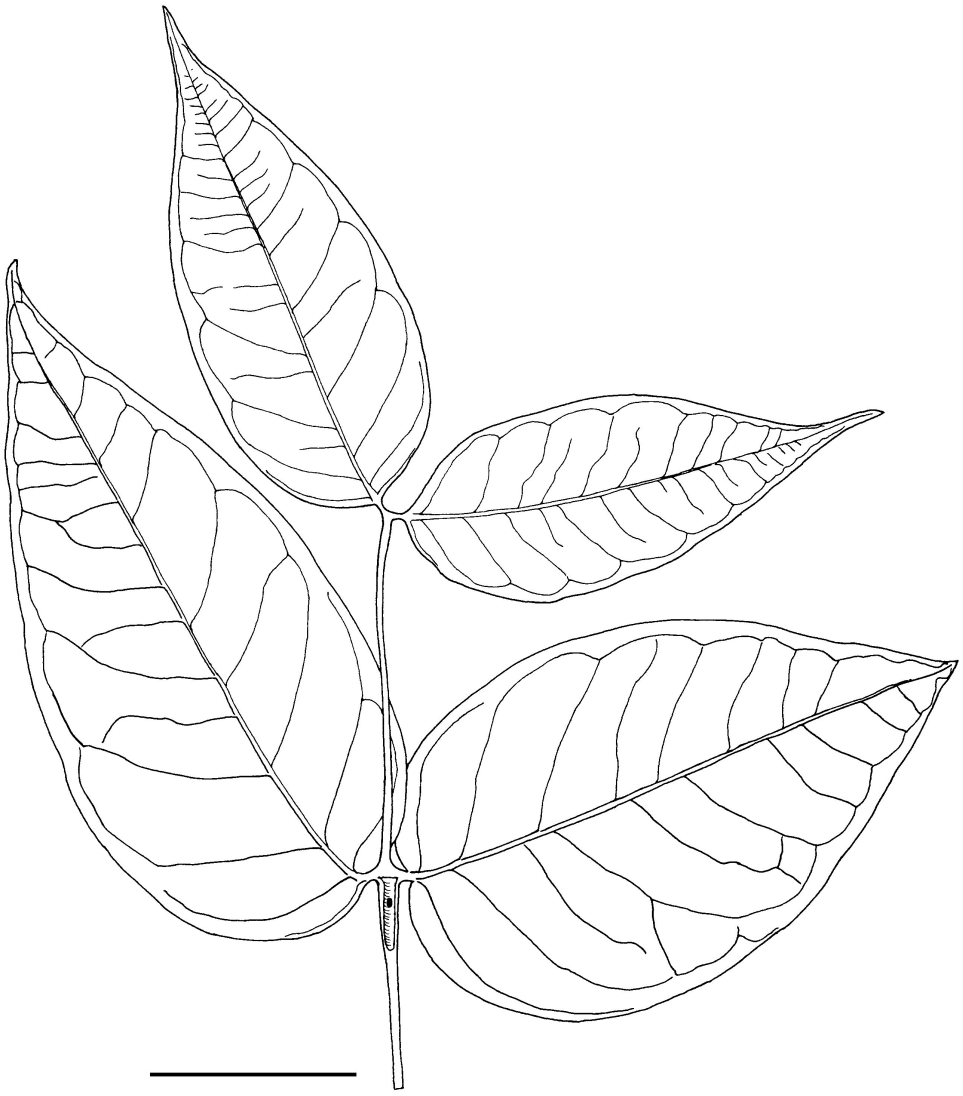


Figure 4-40: Twig of a *Crypteronia griffithii* sapling (0.5 m in height) with a founding chamber of *Cladomyrma maschwitzi* close to the swollen node (modified from AMO-025, Bukit Larut, Perak, Malaysia, leg. J. Moog). In total, the sapling consisted of 15 internodes, of which six harboured a *Cladomyrma* foundress. Scale bar: 5 cm. Drawing: Jürgen Kisch.

The second ant partner, *C. crypteroniae*, is one of the largest *Cladomyrma* species, and colony foundations were collected from young twigs with an average diameter of 6.2 mm ± 1.04 SD (range 4.5–7.9 mm, n=23). This difference in twig sizes used by the two *Cladomyrma* species during colony foundation is also reflected in the nesting space which can be excavated by the worker ants. Figure 4-41 shows how the pith diameter affects the available nesting space for *C. maschwitzi* and *C. crypteroniae*, respectively. The smallest pith canal used by workers of the latter was 1.8 mm across, whereas workers of the former excavated nest chambers in pith canals as small as 1.3 mm (and once even lower) in diameter. Thus, *C. crypteroniae* usually occupies plants > 2 m in height whose new shoots provide pith diameters suitable for colonisation.

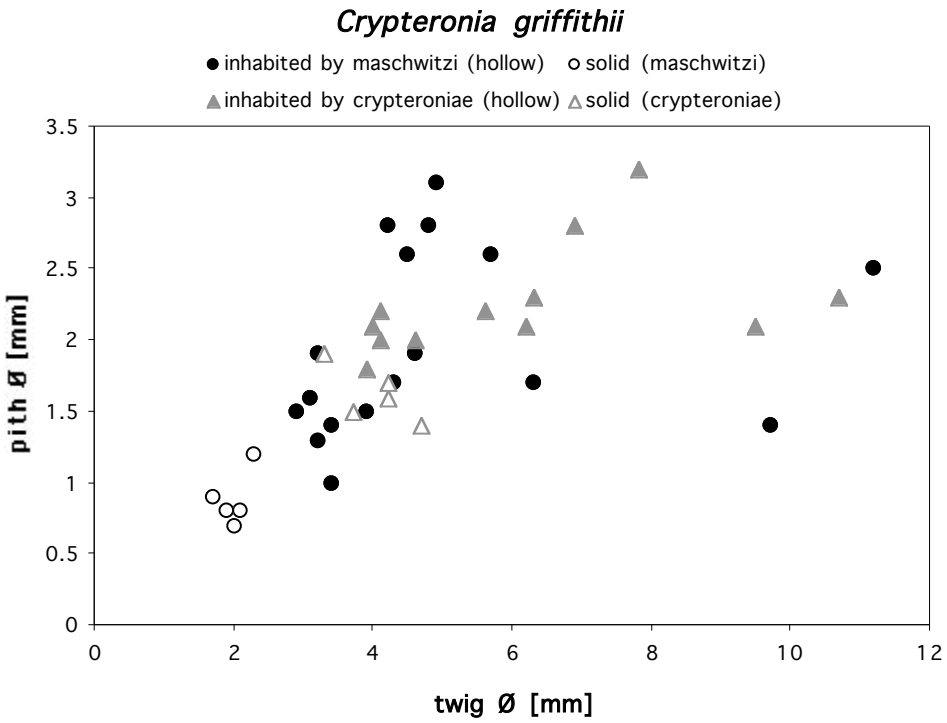


Figure 4-41: Comparison of the nesting space utilised by *C. crypteroniae* and *C. maschwitzi* in twigs (n=39) of the host *Crypteronia griffithii*. Colonised plants sometimes have twig sections which are not used as nest site by the resident ants. The diameters of these twig parts are given as *solid* (open symbols). The diameters of hollowed-out twig parts are given as *inhabited* (filled symbols). The minimum pith diameter necessary to allow the excavation and colonisation of the twigs strongly differs between the two ant species (1.0 to 1.3 mm for *C. maschwitzi*, 1.8 mm for *C. crypteroniae*). [Secondary growth of twigs is indicated by twig/pith ratios of > 2.5.]

Ant occupancy rate: In total, 203 trees of various size (mean tree height 3.7 m ± 5.03 SD, range 0.3–30 m) were checked for occupancy by *Cladomyrma* ants. Overall, occupancy rate was 86% (174), whereas 14% (29) were unoccupied (Fig. 4-42). The height of uninhabited plants exhibited a highly bimodal distribution with 23 saplings (0.3–0.8 m) and 6 adult trees (25–30 m). If only plants >0.5 m are considered, occupancy rate is 93% (174 of n=187). All trees ranging in height from >1 to 15 m were inhabited by *Cladomyrma* ants (100%, n=149). Because sample size of trees belonging to the higher size classes (>10–30 m) was low, I checked herbarium material of Malayan *Crypteronia griffithii* to obtain additional information on colonisation of flowering adult trees. From 33 specimens examined, two showed clearly visible *Cladomyrma* entrance holes, indicating that the specimens were collected from inhabited trees. According to the collectors notes the heights of these flowering trees were 15 and 21 m, respectively. In another 6 herbarium specimens I could not decide with confidence if the trees housed ant tenants or not. Twentyfive specimens showed neither entrance holes nor hollow twigs, thus are regarded as

uninhabited. The very low proportion of colonised adult trees is consistent with the observation that 6 adult *C. griffithii* checked in the field were not occupied by *Cladomyrma* ants. Figure 4-43 presents the pooled data set of both the field and herbarium studies on occupancy rate of Malayan *Crypteronia griffithii* by *Cladomyrma maschwitzi*, and it becomes apparent that the association between *Crypteronia* and *Cladomyrma* strongly decreases in plants of higher tree size. Therefore, I conclude that the association dispands with the age of the host tree.

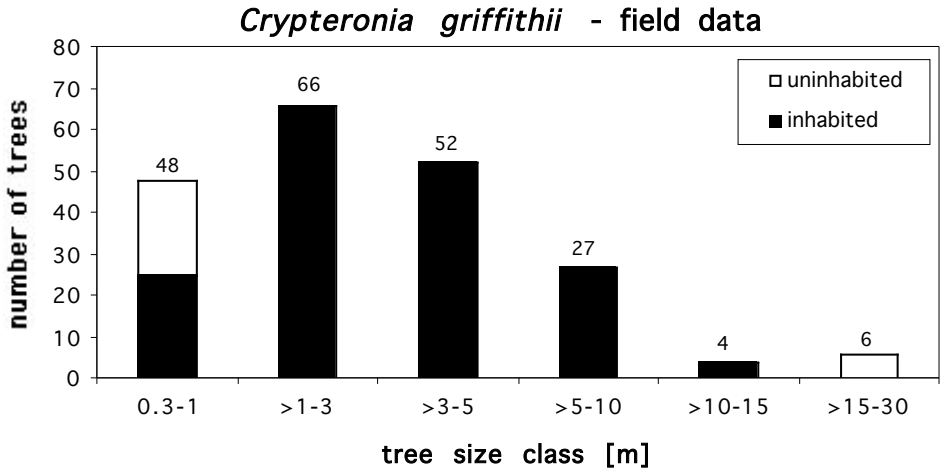


Figure 4-42: Occupation frequency of *Crypteronia griffithii* by *Cladomyrma crypteroniae* and *C. maschwitzi* (pooled) as a function of tree height. Included are field data (n=203) from all regions of the host's distribution (Borneo, Malay Peninsula and Sumatra). Occupied trees n=174 (86%); unoccupied trees n=29 (14%).

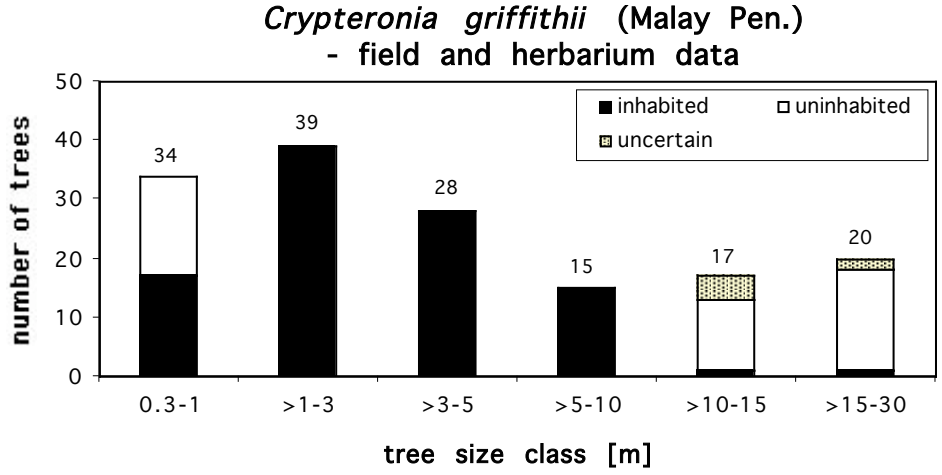


Figure 4-43: Occupation frequency of *Crypteronia griffithii* by *Cladomyrma maschwitzi* as a function of tree height. Included are field (n=120) and herbarium(n=33) data from the Malay Peninsula. All herbarium data fall into the size classes >10–15 and >15–30. Some herbarium specimens were of an uncertain colonisation status. Occupied trees n=101 (66%); unoccupied trees n=46 (30%); trees with uncertain occupation status n=6 (4%).

The pattern becomes more complex when we look at the occupancy rate in the geographic areas of Borneo and Sumatra, where a second *Cladomyrma* species, *C. crypteroniae*, competes with *C. maschwitzi* for the same host plant (Fig. 4-44). Here, the latter appears to be excluded from trees of higher size classes as compared to the Malay Peninsula (see above, Fig. 4-43), implying a succession of ant occupants.

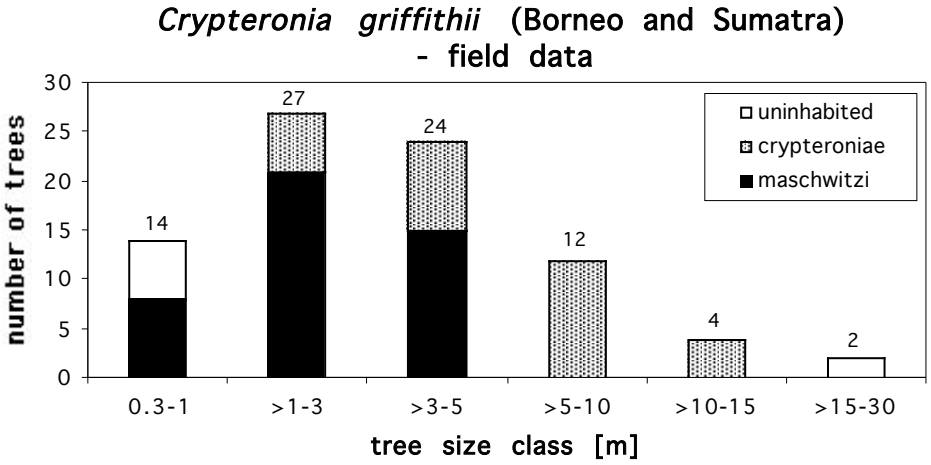


Figure 4-44: Occupation frequency of *Crypteronia griffithii* by *Cladomyrma crypteroniae* and *C. maschwitzi* as a function of tree height. Included are field data (n=83) from Borneo and Sumatra. Trees occupied by *C. maschwitzi* n=44 (53%); trees occupied by *C. crypteroniae* n=31 (37%); unoccupied trees n=8 (10%).

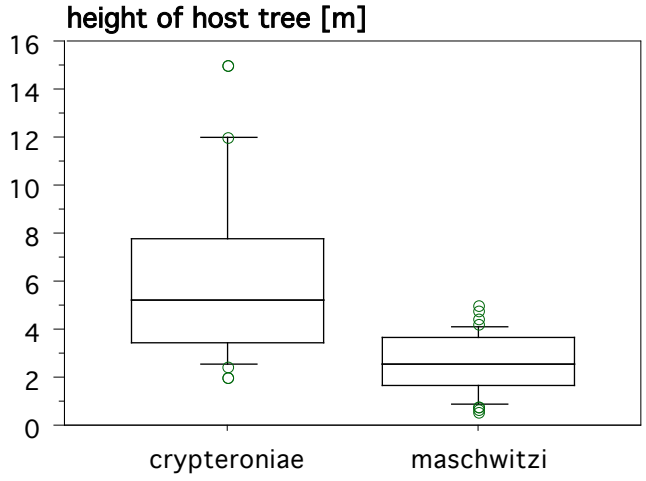


Figure 4-45: Comparison of host size inhabited by *Cladomyrma crypteroniae* (n=31) and *C. maschwitzi* (n=44). The difference in tree height between trees inhabited by *C. crypteroniae* or by *C. maschwitzi* is highly significant ($P < 0.0001$; Mann-Whitney U-test). *Box-whisker plots*: centre line denotes median value, the box encloses the inner two quartiles (25^{th} and 75^{th} percentile), and the whiskers display the 10^{th} and 90^{th} percentile, small circles denote outliers.

In Borneo and Sumatra, all trees between > 5 to 15 min height were occupied by *C. crypteroniae*, suggesting that this species is competitively dominant over *C. maschwitzi*. Tree size occupied by *C. crypteroniae* and *C. maschwitzi* significantly differed between the two species ($P < 0.0001$, Mann-Whitney U-test; mean tree $height_{crypteroniae}$ 6.1 m ± 3.59 SD versus mean tree $height_{maschwitzi}$ 2.6 m ± 1.26 SD; Fig. 4-45).

However, the smallest tree found harbouring *C. crypteroniae* was 2 m tall and, therefore, *C. maschwitzi* dominates on *Crypteronia* saplings. As shown above (Fig. 4-41), this is linked to the available nesting space, which does prevent *C. crypteroniae* from excavating and entering small-sized stems of saplings. In conclusion, the smaller size of *C. maschwitzi* facilitates priority of access to the host plant resource and allows persistence on the host until reaching the reproductive stage (mature colonies with alate sexuals have often been found). It will be interesting to study in detail (i) how the displacement of *C. maschwitzi* by *C. crypteroniae* takes place, and (ii) whether the observed pattern is the consequence of direct or indirect interactions between the two species. The alternative hypothesis, i.e., that the host plant is locally so abundant that founding queens do not compete for it, can be excluded both by the high occupancy rate and by the regular occurrence of multiple foundations on individual host plants.

Herbarium study: The examination of herbarium specimens (n=90) of *Crypteronia griffithii* from all regions of its distribution (Borneo, Malay Peninsula and Sumatra) seem to contradict the results obtained in the field. Occupancy rate was very low (9%) and most specimens (83%) did not show any signs of ant inhabitation. The remaining specimens (8%) could not unambiguously classified as colonised or not. Although they possessed hollow twig sections, they lacked ant entrance holes and the origin of the hollows was unclear. The difference between occupancy rates found in the field and those derived from the herbarium material is easily explained by the fact that the herbarium specimens were collected from adult flowering plants. Thus, the very low proportion of colonised adult trees is consistent my observations in the field (all six trees >15–30 m lacked ant occupants).

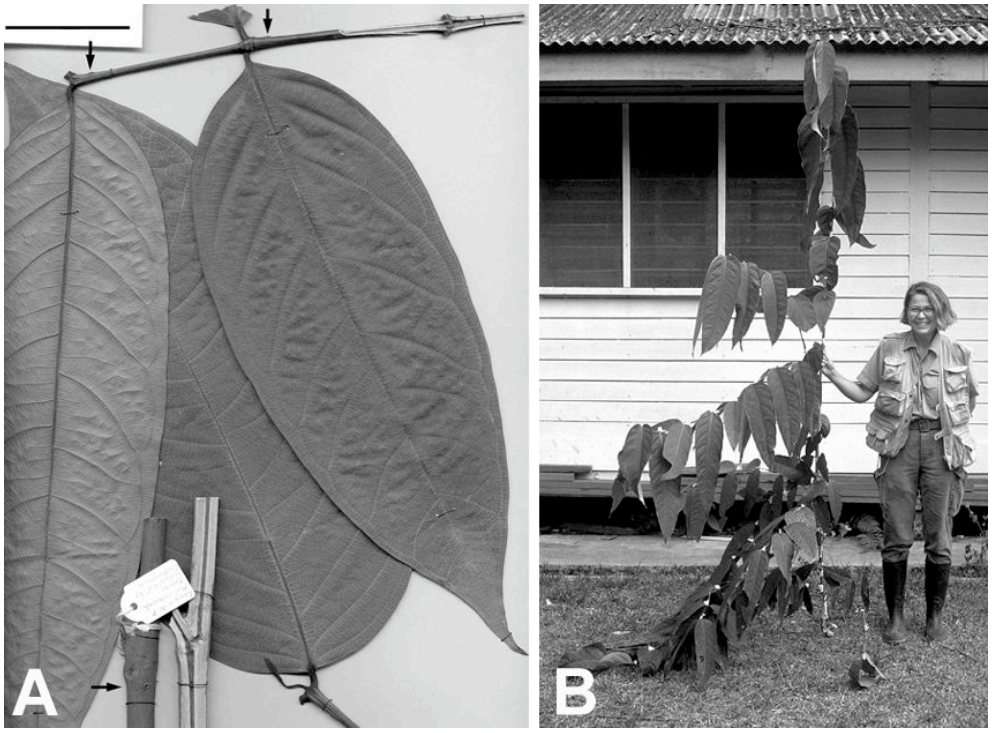


Figure 4-46: *Crypteronia griffithii*. **A**: dried specimen of a small tree, 2 m tall, inhabited by *Cladomyrma maschwitzi* (AMO-075, Lambir Hills NP, 4th division, Sarawak, Borneo, leg. J. Moog). Arrows indicate the position of ant entrance holes. They are always located laterally below the nodes. Longitudinally dissected stem sections show the nest chambers. Scale bar: 5 cm. **B**: Small tree, 2.4 m in height, cut off to examine the nest structure of *Cladomyrma maschwitzi* (Ulu Gombak, Malay Peninsula). The plant was occupied by the ants in its total length (note the tape that is used to seal entrance holes). All branches are directed to one side because the tree grew at a forest edge facing a small logging road.

Crypteronia macrophylla Beus.-Osinga

Figure 4-47

Tree, up to 25 m; uncommon but locally frequent; in primary and advanced secondary forest, sometimes near river banks; 200–1,200 m altitude (BEUSEKOM-OSINGA 1977, PEREIRA 1996). Distribution: Borneo (Sarawak and Kalimantan only). Note: Not seen in the field.

Ant-housing structures: According to herbarium material, the stems and twigs of *C. macrophylla* closely resemble those of *C. griffithii*. On average, the twig diameter increased from mid-internode to the node by 3.8 mm, but sample size was low (n=5).

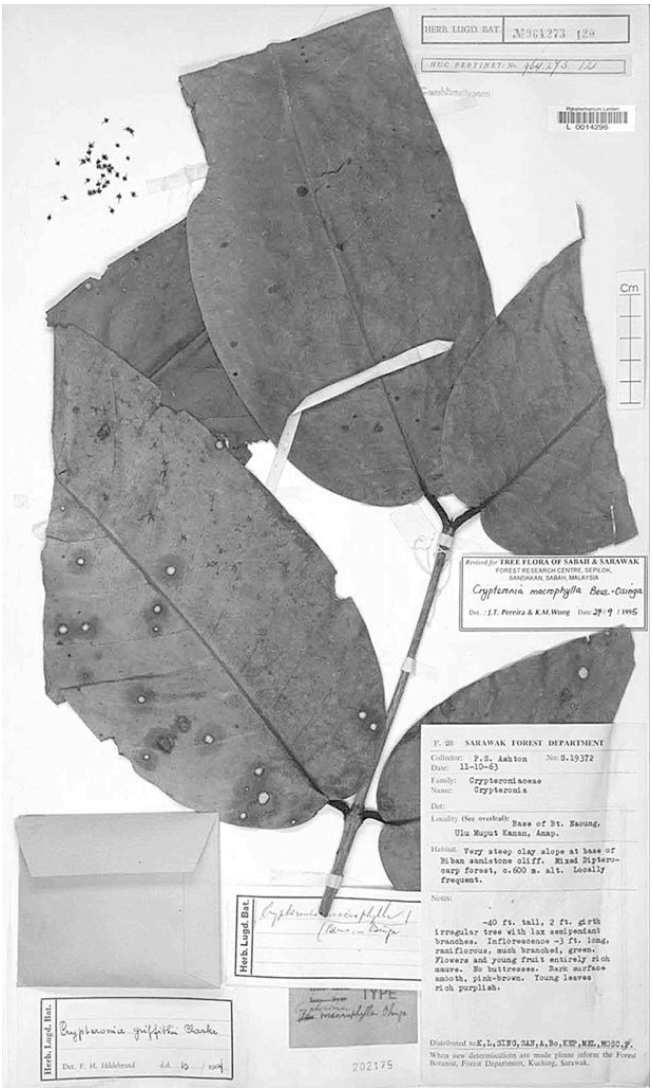


Figure 4-47: Herbarium specimen of *Crypteronia macrophylla* (S.19372, holotype, Anap, 4th division, Sarawak, Malaysia, Borneo, leg. P. S. Ashton). The type has hollow twigs and lateral ant entrance holes below the nodes. Scale bar: 5 cm. Source: http://www.nationaalherbarium.nl.

Ant inhabitants: The two revisions of *Crypteronia* mention for *C. macrophylla* a frequent colonisation of young branches by unidentified ants (BEUSEKOM-OSINGA 1977, PEREIRA 1996). According to the herbarium specimens examined, the ant partner of *C. macrophylla* appears to be a *Cladomyrma* species. Entrance holes in internodes are, with respect to size, form and position, identical to those observed in *C. griffithii*. Field trips to some of the collecting sites, however, have not been successful due to the rapid and destructive exploitation of formerly untouched primary forest (BROOKFIELD et al. 1990). I suggest that the *Cladomyrma* species inhabiting *C. griffithii* are the colonisers of *C. macrophylla* as well.

Ant occupancy rate derived from herbarium material: Of 20 specimens examined, 18 (90%) exhibited unambiguous traits of ant colonisation, and only for two specimens (10%) the signs of former ant occupancy were less clear ('uncertain' colonisation status). This high occupancy rate stands in striking contrast to *C. griffithii* where the herbarium material did not reflect the high proportion of colonisation seen in the field. The most plausible factor explaining this difference is that the two species strongly differ in the onset of reproduction. *Crypteronia macrophylla* appears to flower much earlier than *C. griffithii* and thus fertile specimens are collected at a stage where the resident *Cladomyrma* colony is still present. Support for this assumption comes from the comparison of tree height given on herbarium labels: the two species significantly differed in tree height (Fig. 4-48; Mann-Whitney U-test, $P < 0.0001$).

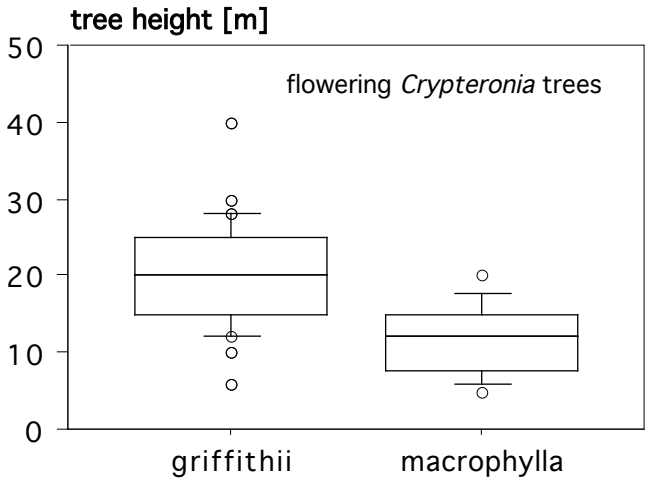


Figure 4-48: Comparison of tree size between herbarium specimens of flowering *Crypteronia griffithii* (n=58) and *C. macrophylla* (n=13). Mean tree height *griffithii* 20.3 m ± 6.81SD, range 6–40 m; mean tree height *macrophylla* 11.5 m ± 4.45 SD, range 5–20 m; $P < 0.0001$ (Mann-Whitney U-test). [For explanation of box-whisker plots see fig. 4-45.]

According to herbarium notes, *C. macrophylla* also significantly differs from *C. griffithii* in its altitudinal range ($P < 0.0001$, Mann-Whitney U-test). On average, *C. macrophylla* was collected at an elevation of 724 m ± 315.8 SD (n=13), whereas *C. griffithii* was found at a mean altitude of 198 m ± 165.6 SD (n=58). An effort should be made to find *C. macrophylla* in the field and to test whether the phenological and ecological differences between the two species as revealed by the herbarium data are linked to differential patterns of ant association.

4.3.7. Putranjivaceae

Drypetes longifolia (Bl.) Pax & Hoffm.

Figures 4-49, 4-50, 4-51, 4-52A

Small tree to 20 m, rarely up to 30 m; rare in the Malay Peninsula, locally common in Borneo; in primary and advanced secondary forests; lowlands to 1,300 m altitude (AIRY SHAW 1975, pers. observation). Distribution: India, Sri Lanka, Andamans, Myanmar, Malay Peninsula, and throughout Malesia to New Guinea. Note: Recently, it became clear that the traditional assignment of the genus *Drypetes* to the Euphorbiaceae cannot be maintained (TOKUOKA & TOBE 1999), and *Drypetes* is now transferred to the Putranjivaceae (SAVOLAINEN et al. 2000, THORNE 2002).

Figure 4-49: *Drypetes longifolia* from the Malay Peninsula. **A**: tree, 6.5 m tall, with drooping branches, atypically growing among bamboo; **B**: twig with domatia of a 4 m tall tree growing in the understorey. From a distance, the domatia are hardly noticeable.

Ant-housing structures: Swellings regularly occur along the twigs (Fig. 4-50, 4-51A-B) of Bornean and Malayan *Drypetes longifolia*, and they may run over 1 to 2.5 internodes. Saplings of the Bornean population developed their first domatium at an average height of 0.34 m ± 0.09 SD (range 0.23–0.49, n=8), whereas domatia of Malayan saplings first occurred at a mean height of 0.64 m ± 0.11 SD (range 0.5–

0.78, n=6). The diameter of the pith canal within the fistulose domatia is distinctly increased compared to the unswollen stem sections. The pith tissue inside these domatia consists of white and soft parenchymatic cells compared to the rather hard and compact ones found in other stem parts (Fig. 5-51C-D). Ants can easily remove the soft dilated pith to create a nesting chamber. In adult trees, the primary stem diameter is mostly sufficiently large to allow the excavation of the branches and twigs throughout their length. Although prostomata are not developed, the wood thickness is generally smaller at the domatia (Fig. 4-51C). All saplings from the Malay Pen. (n=3) and Borneo (n=1) planted in a greenhouse produced domatia in the absence of ants.

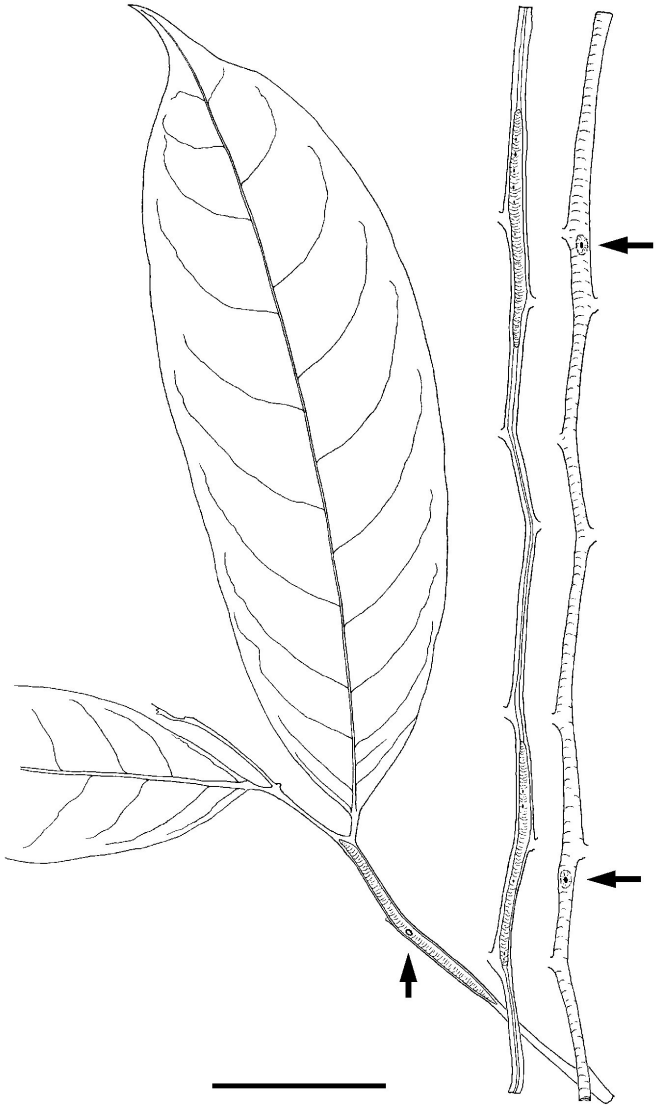


Figure 4-50: Dissected domatia of young *Drypetes longifolia* (modified from AMO-053, 3 m tall, right, and AMO-054, 0.73 m tall, left; Malay Peninsula, leg. J. Moog). Arrows indicate position of ant entrance holes at the swollen, hollowed out twig sections (domatia). Note the increase of the pith diameter and the smaller wood thickness at the domatia. Scale bar: 5 cm. Drawing: Kisch.

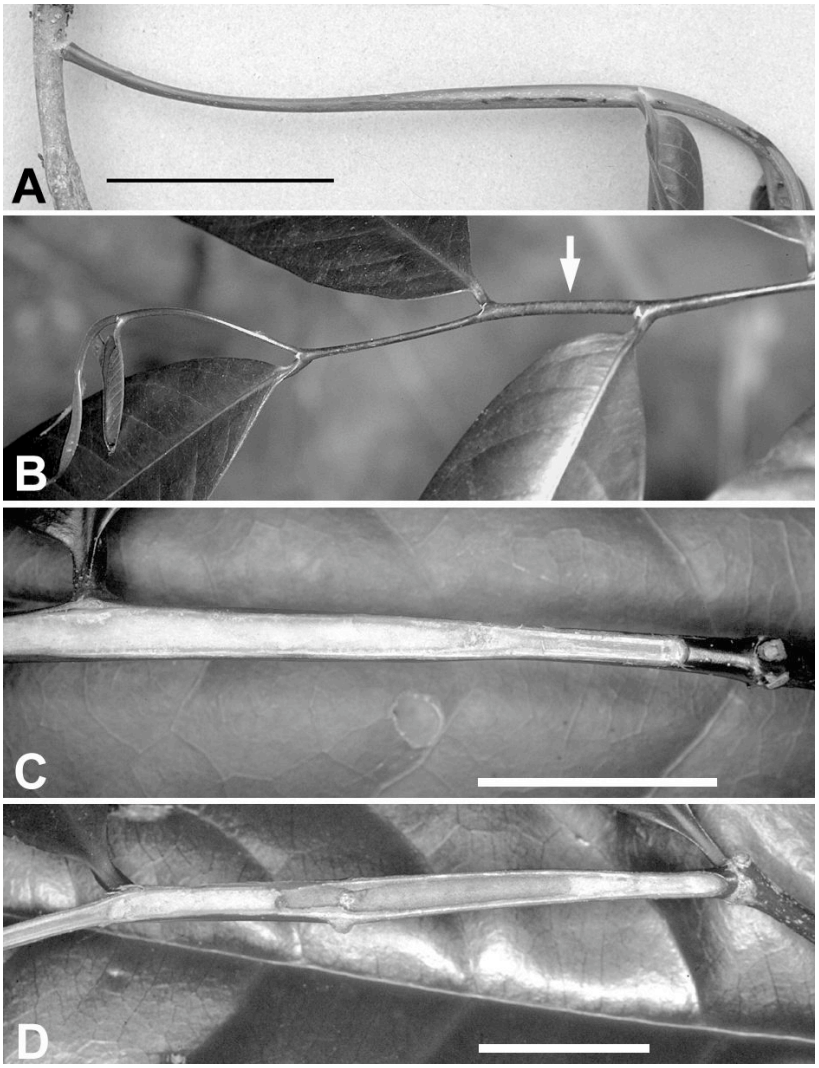


Figure 4-51: Domatia and pith of *Drypetes longifolia* (Malay Peninsula). **A**: young developing swollen shoot of a 6.5 m tall tree; **B**: small twig of a treelet (3 m) with a domatium (arrow); **C**: dissected twig of a sapling (1.1 m) with an uninhabited domatiumshowing the abrupt change in pith diameter and structure; **D**: dissected twig of a sapling (0.73 m) with a domatium partly hollowed out by a colony founding *Cladomyrma* queen. Scale bar A: 5 cm; C and D: 2 cm.

The domatia of Bornean and Malayan *D. longifolia* appear to differ in several aspects. In Bornean saplings, the first domatia are produced at an earlier stage (ca. 0.3 versus 0.6 m height), they tend to be shorter and the swellings are often restricted to one internode only. In addition, Bornean trees seem to produce twigs with a greater primary diameter much earlier in their ontogeny than the Malayan trees, thus allowing the ants to chew nest tunnels throughout the length of the twigs at an earlier stage of the association. If these differences represent traits of taxonomic significance has yet to be studied. The Bornean population of *D. longifolia* has formerly been described as a separate species, *D. myrmecophila* Merrill (see below).

Ant inhabitants: In the Malay Peninsula, two *Cladomyrma* species, *C. petalae* and *C. nudidorsalis* (AGOSTI, MOOG & MASCHWITZ 1999), are known to occupy *D. longifolia* at very high frequencies. In Borneo, at least three species, *C. andrei*, *C. hobbyi*, and *C. yongi*, have been found in *Drypetes*, the latter ant species being the most dominant in the collections (AGOSTI, MOOG & MASCHWITZ 1999). Probably a fourth species (which may be a yellow form of *yongi*) inhabits *Drypetes longifolia* and possibly *D. fusiformis* Airy Shaw in East Borneo (see page 39). Outside Borneo and the Malay Peninsula, *Drypetes longifolia* is not occupied by *Cladomyrma* ants. [Note that some herbarium specimens of New Guinean *D. longifolia* possessed hollow stem sections and entrance holes indicative of previous ant occupation but the regularity of ant association is unknown.]

Onset of ant occupation: *Cladomyrma* foundress ants colonise saplings shortly after domatia are present (earliest 0.23 m Borneo, 0.5 m Malay Pen.) During my studies I found only 2 saplings which already had produced domatia but still lacked ant tenants (Borneo: 0.36 m plant with 2 domatia; Malaya: 1.1 m plant with 4 domatia). Multiple colony initiations are the rule but a single colony dominates the tree at a later stage. Ant workers of growing colonies enlarge the initial domatia chambers by excavating also the less soft pith of non-dilated stem parts, provided the primary pith diameter is large enough to allow the passage of the ant workers. Consequently, the proportion of a plant occupied increases with age of the association (e.g., for five Malayan plants: 25%/0.7 m height, 34%/2.7 m, 38%/4.1 m, 46%/6.5 m, and 62%/7.5 m).

Ant occupancy rate: From a total of 116 plants found in the field (mean tree height 2.8 m ± 2.25 SD, range 0.26–14 m), 95% (110) were occupied by *Cladomyrma* ants. Occupancy rate remains high if Bornean and Malayan populations are considered separately: 95% (96 of n=101) and 93% (14 of n=15), respectively. The frequency of occupation reached 100% in plants >0.5 (Borneo) and >1.1 m tall (Malay Pen.).

Herbarium study and taxonomic problems: Myrmecophily was first reported by MERRILL (1929) for the two Bornean *Drypetes* species, *D. macrophylla* (Bl.) Pax & Hoffm. and *D. myrmecophila* Merr. However, AIRY SHAW (1969, 1975) later synonymized these two species with *D. longifolia* on the base of continuous variation of leaf base and leaf size, whilst leaf venation, flowers and fruit appeared to him not distinctive between the three species. In my opinion, the species concept applied by AIRY SHAW to *Drypetes longifolia* is probably too broad, since I recognised that all herbarium specimen from India (including Sri Lanka and Andamans), Continental Asia, and Sumatra clearly differ from the Malayan species by a smaller leaf size and twig diameter, combined with differences in the leaf base. If these discontinuous

characters constitute a base for drawing distinctions among these populations at the species level should be answered in future revision of the genus. Moreover, the Bornean form of *Drypetes longifolia* appears to be distinct from the Malayan form by differences in vegetative characters such as domatia formation (see above) and leaf form and size (Fig. 4-52).

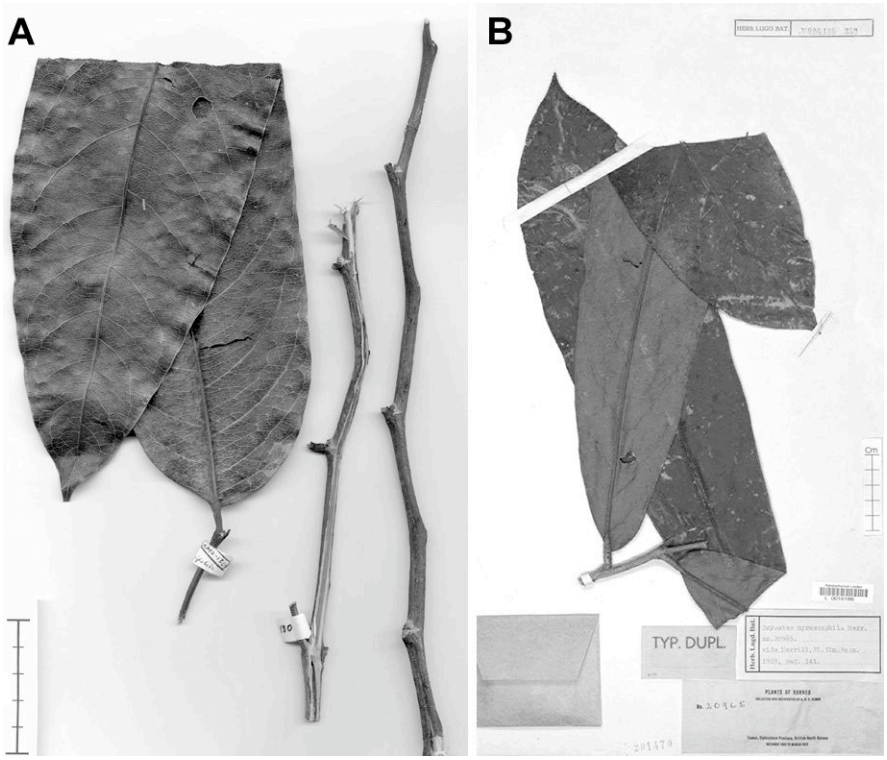


Figure 4-52: Dried specimens of *Drypetes longifolia* sensu lato from the Malay Peninsula (A) and Borneo (B). **A**: tree 7.5 m tall, twigs hollow, inhabited by *Cladomyrma petalae* ants, AMO-130, Fraser's Hill, leg. Ute Moog; **B**: type of *Drypetes myrmecophila* Merr., Elmer 20965, twig hollow with ant entrance hole, Tawau, Sabah, Borneo, leg. A. D. E. Elmer. Scale bars: 5 cm. These two specimens represent the typical appearance of adult trees of Malayan and Bornean *D. longifolia*. Leaves of the latter are usually elongate, obovate, with a strongly assymetric leaf base. Source for B: http://www.nationaalherbarium.nl.

Overall, I examined 178 herbarium collections of *Drypetes longifolia* sensu lato. All specimens seen from India, Sri Lanka and the Andamans (n=4), Thailand (2), Philippines (3), Sumatra (16), Java (24) and Sulawesi (5) lacked signs of former ant occupation. In contrast, a certain percentage of the Bornean (n=70), Malayan (35) and New Guinean (19) material bore distinctive ant entrance holes: 70%, 14% and 16%, respectively. A number of specimens were seen which had hollow stems but the stem parts were too short to show an entrance hole and thus their colonisation status was classified as 'uncertain'; i.e., Borneo 9%, Malay Peninsula 17%, and New Guinea 5%.

For the Bornean material, results of the herbarium studies confirmed those of the field studies but this did not hold for the Malayan material. The comparatively low proportion of occupied herbarium specimens is assumably attributable to the sampling of distal, non-swollen stem parts by the collectors. Field studies in New Guinea should clarify whether the percentage of ant-occupied herbarium specimens indicates a regular association with ants.

Several of the collectors noted the presence of ants: 1.) CLEMENS 40671, Sabah, Borneo: "*stems symbiosis with ants*"; 2.) KEP 55235, Sabah, Borneo, leg. H. G. KEITH: "*twigs have a hole in the centre along the pith, sometimes used as pipes by natives of the interior*"; 3.) S.19762, Sarawak, Borneo, leg. P. CHAI: "*twigs hollow inhabited by ants*"; 4.) JD 7050, Brunei, Borneo, leg. J. DRANSFIELD: "*twigs grey, hollow, full of ants*; 5.) NGF 10014, Papua New Guinea, leg. K. J. WHITE: "*smell of formic acid*"; and 6.) NGF 10313A, Papua New Guinea, leg. K. J. WHITE: "*pith tunnel inhabited by small ants*". One specimen, AA 2071 (East Kalimantan, Borneo, leg. AMBRAINSYAH & ARBAINSYAH), examined at Leiden, contained the remains of *Cladomyrma* workers in the hollow twigs.

Drypetes fusiformis Airy Shaw

Figures 4-53, 4-54B

Tree to 35 m; rare; in primary forests, sometimes near riversides; up to 200 m altitude (AIRY SHAW 1965, 1969, 1975; and herbarium labels). Distribution: Borneo (Sabah, East Kalimantan). Note: Known from herbarium specimens and possibly seen in the field (see below).

Ant-housing structures: Specimens of *D. fusiformis* examined at the Leiden herbarium have twigs that appear to lack swollen sections (Fig. 4-53). However, the primary diameter of these twigs is often sufficiently large to allow the tunneling of the pith by ants throughout the twig's length. I have not seen material collected from saplings, hence I do not know if domatia are developed during the early stages of the plant's ontogeny.

Ant inhabitants: Some herbarium specimens possess ant entrance holes whose size, shape and distribution along the twigs strongly indicate that a *Cladomyrma* species is the regular coloniser of *D. fusiformis*. If the plants I found at Sepilok Forest Reserve (Sabah, Borneo) are true *D. fusiformis*, the *Cladomyrma* species bears a strong

resemblance to a yellow form of *C. yongi* (see page 39). Whether it represent a new species or not has yet to be clarified.

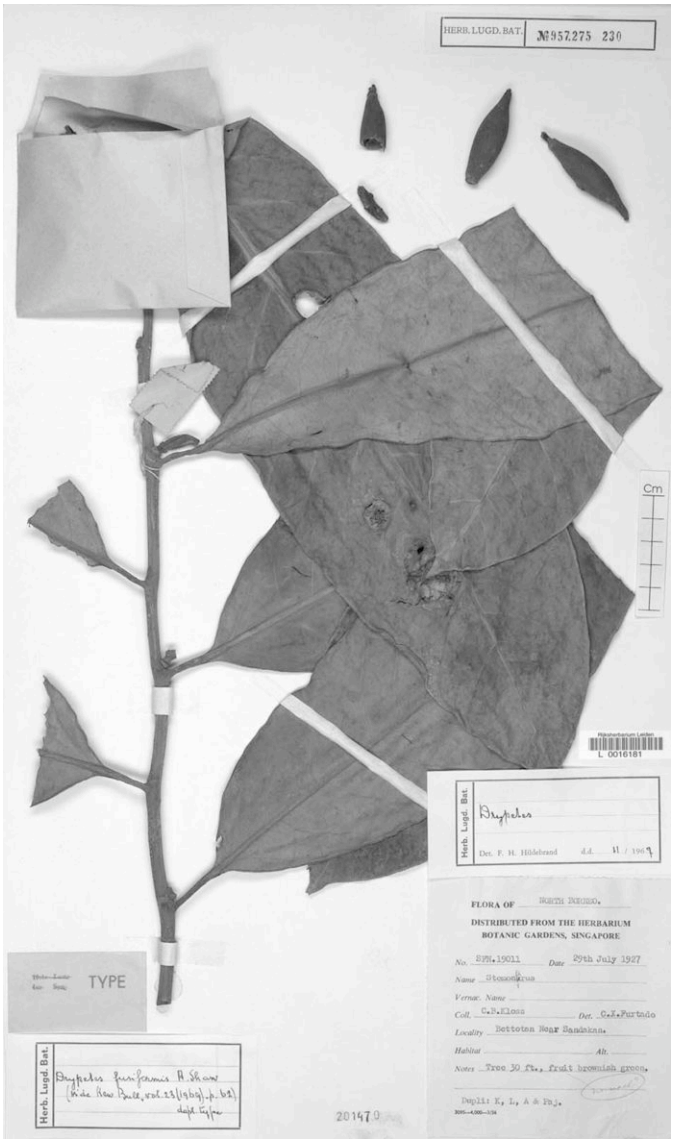


Figure 4-53: *Drypetes fusiformis*. Dried specimen collected from a tree 9 m high (isotype, SFN 19011, Bettotan, Sandakan, Sabah, Borneo, leg. C. B. Kloss). Note the long petioles and the weakly unequal leaf bases. Scale bar: 5 cm. Source: http://www.nationaalherbarium.nl.

Ant occupancy rate derived from herbarium material: Two of 5 specimens examined (40%) possessed ant entrance holes and hollow twigs (SFN 19011, SAN 80996). The remaining 3 samples from East Kalimantan, however, lacked signs of ant occupation, i.e., KOSTERMANS 6978 and 10610, and B-11759 (leg. KATO, OKAMOTO & UEDA). A sixth specimen, JBS 97 (leg. SUGAU et al.), collected in the Ranau area

(Sabah) is only known from an internet source (www.nationaalherbarium.nl), but ant occupancy is not mentioned. In the Sepilok Forest Reserve near Sandakan (Sabah), I came across seven sterile plants somewhat recalling *D. fusiformis* as known from the herbarium studies. These plants appeared to be intermediate between typical Bornean *D. longifolia* and *D. fusiformis* (Fig. 4-54).

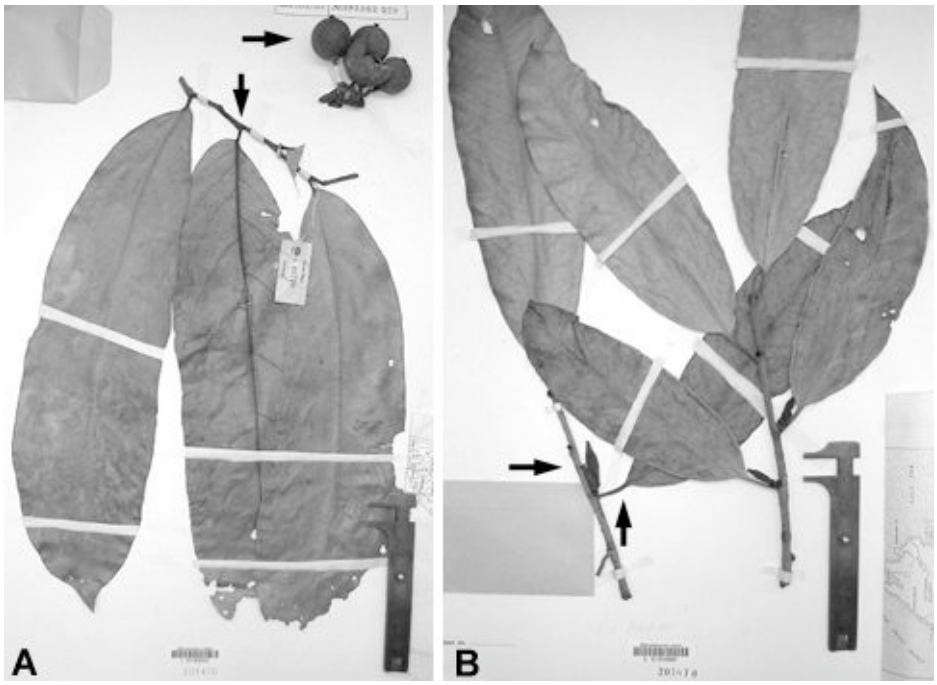


Figure 4-54: Comparison of Bornean *Drypetes longifolia* (A) and *D. fusiformis* (B). **A**: specimen collected from a tree 9 m tall, S.46720, Dulit Range, Sarawak; **B**: specimen from a tree 8 m tall, SAN 80996, Segaluid Lokan Forest Reserve, Sandakan, Sabah, leg. Aban & Leopold. Calliper rule set to 1 cm. Note the differences in the leaf base, fruits and petiole length (arrows).

The two species *D. longifolia* and *D. fusiformis* significantly differ in the mean length of the petiole (P = 0.0005; df = 13, unpaired Student t-test; equality of variances is met (F-test)). Bornean *D. longifolia* has, on average, a petiole length of 9.0 mm ± 1.97 SD (range 6–13 mm, n=48 of 10 plants), whereas *D. fusiformis* has distinctly longer petioles (mean 16.1 mm ± 3.78 SD, range 9–22 mm, n=32 of 5 plants). The seven Sepilok plants, however, bore petioles of intermediate length (mean 12.3 mm ± 1.53 SD, range 11–14 mm). In some characters, such as the unequal leaf base and the venation of leaf underside, the Sepilok plants more closely resembled Bornean *D. longifolia*, but in others, e.g. leaf size and leaf shape, they came closer to *D. fusiformis*. Both species are known from the Sepilok Forest Reserve and, at present, the identification of the seven plants harbouring the "*yellow yongi*" is not possible.

4.3.8. Rubiaceae

Neonauclea Merr.

The genus *Neonauclea* as currently circumscribed consists of 65 tree species and is predominantly distributed in Malesia, only four species occur in continental Asia (RIDSDALE 1989). At least 17 (28%) of the 61 Malesian species possess conspicuous internodial domatia swellings which have been reported to be inhabited by ants (SCHUMANN 1889, HAVILAND 1897, BEQUAERT 1922, RIDSDALE 1989). According to Ridsdale (l. c.), domatia bearing species occur on Sumatra (two species), Borneo (8), Sulawesi (6), including its small neighbour islands, and the southern Philippines (1+). Outside Borneo, *Neonauclea* is inhabited by *Crematogaster* species (BEQUAERT 1922, MASCHWITZ & FIALA 1995; pers. observation). In contrast, the eight Bornean species appear to be regularly colonised by *Cladomyrma* ants (this study; Fig. 4-55).

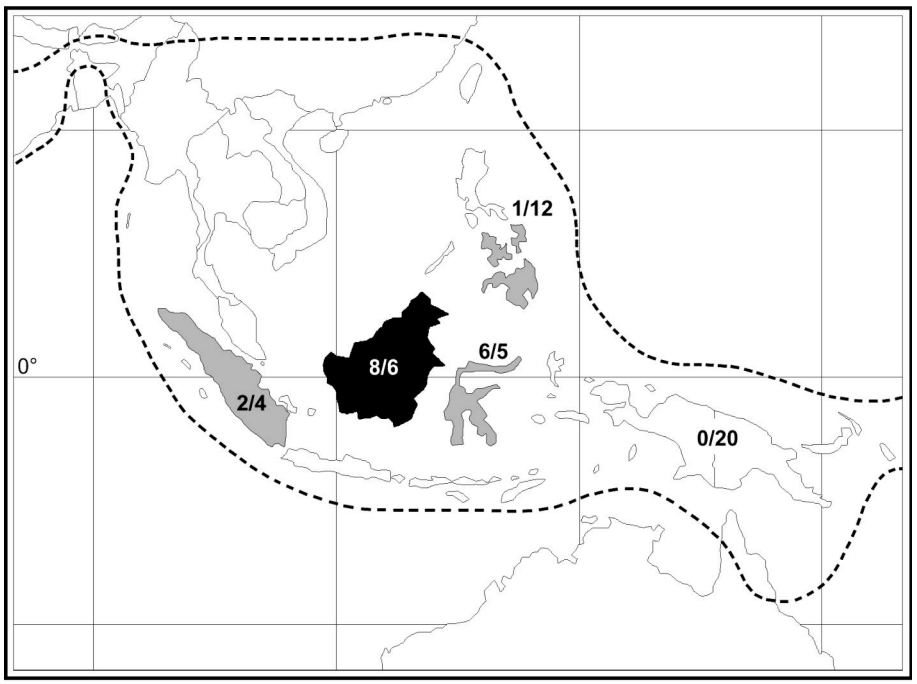


Figure 4-55: Map showing the distribution of *Neonauclea* in Southeast Asia (*broken line*). *Black and grey landmasses* illustrate the distribution of *Neonauclea* species bearing myrmecodomatia; *black* areas (Borneo) represent the distribution of species inhabited predominantly by *Cladomyrma* ants and *grey* areas (Sumatra, Sulawesi, southern Philippines) the one of species inhabited by *Crematogaster*. Numbers of myrmecophytic/non-myrmecophytic *Neonauclea* species are indicated for each of these areas as well as New Guinea.

In Sabah and Sarawak, I was able to identify 5 species inhabited by *Cladomyrma* ants: *N. borneensis* Ridsd., *N. gigantea* (Valeton) Ridsd., *N. longipedunculata* Merr., *N. paracyrtopoda* Bakh. f. & Ridsd., and *N. pseudocalycina* Ridsd. However, as the determination keys for *Neonauclea* species (RIDSDALE 1989) are primarily based on

floral characters, I was unable to identify the majority of collections which came from saplings. Some of the few vegetative characters (e.g., stipules) RIDSDALE considers useful are unknown for several species. It is possible that the unidentified specimens – for which I provisionally use the informal species names sp. A to E– are new species or identical to some of the eight Bornean myrmecophytic *Neonauclea* species (e.g., *N. artocarpoides* Ridsd., *N. calcarea* Ridsd., and *N. excelsioides* Ridsd.).

Because species determination of saplings was in many cases impossible and because domatia formation appeared to be more or less uniform among myrmecophytic Bornean *Neonauclea* species, I will first present an overall account of these species with respect to ant-housing structures, ant inhabitants, onset of ant occupation and occupancy rate, followed by a description of each species according to herbarium and field studies (if available).

Ant-housing structures: The presence of swollen internodes is a constant character in myrmecophytic *Neonauclea* species. *N. cyrtopoda* from Sumatra kept in a greenhouse at Ulu Gombak (Malay Peninsula) produces domatia in the absence of ants since its planting seven years ago. Likewise, RIDSDALE (1989) reported that Sulawesian *N. celebica*, cultivated at Bogor (Java), hence in an area where the local species do not have domatia, still has the typical swellings. Cuttings of the latter species kept at Frankfurt University also continue to produce caulinary swellings since several years, although ant tenants are lacking. Domatia formation has also been observed in saplings of *Neonauclea gigantea* (0.4–0.8 m tall, n=4) which were grown in an ant-exclusion environment at Poring Hot Springs (Sabah).

In all species the domatia are arranged along the branches in a very characteristic way. New swellings develop only in the basal internode of a new branch or twig (Fig. 4-56A-B), whereas the main stem axis remains free of domatia. A domatium is formed by a somewhat spindle-shaped hypertrophy in the distal half of the internode. Across 17 species measured (herbarium and field data), a domatium occupies 40.5% ± 11.33 SD of the internode length (range 17–71%; n=105). In young internodes, the primary diameter is increased at the swollen area relative to the proximal, unswollen internode section, on average, by 4.4 mm ± 0.14 SD (range 1–7.5 mm; 12 species measured; n=47). In cross section, a young domatium is broader than high, but secondary growth changes the size ratio and the domatium becomes higher than broad (Fig. 4-57). This is due to the maintenance of 'prostomata', i.e., thin-walled zones of the domatium, where ants preferably chew their entrance holes. The prostomata have the form of a straight line running the entire length of the domatium on each lateral side (Fig. 4-60).

Figure 4-56: Regular distribution of domatia within *Neonauclea* trees. **A**: *N. gigantea*, Borneo; **B**: *N. cyrtopoda*, Sumatra. After branching off, the basal internode of a each branch or twig produces a domatium (arrows). The main axis (trunk) is always free of domatia.

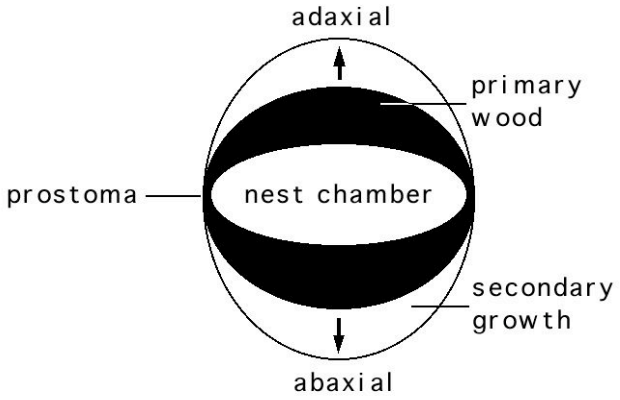


Figure 4-57: Schematic cross section of a domatium of *Neonauclea*. In transverse section, a young domatium is broader than high (primary wood; black). By secondary growth the domatium becomes higher than broad. The thin wood sections at both lateral sides are maintained throughout plant ontogeny and serve as prostomata for ants which preferentially chew their entrance holes at these positions.

Myrmecophytic *Neonauclea* saplings initiate branches –and hence domatia– already at a low height. Branching/domatia production was observed in plants earliest at 0.32 and latest at 1.3 m height. As shown in Fig. 4-58, the number of domatia per plant of a given height may vary considerably (e.g., from 12 to 42 in plants 4.5 m tall) and is dependent on the degree of ramification which, in turn, can be influenced by factors such as light regime, growth conditions, plant competition or herbivore pressure.

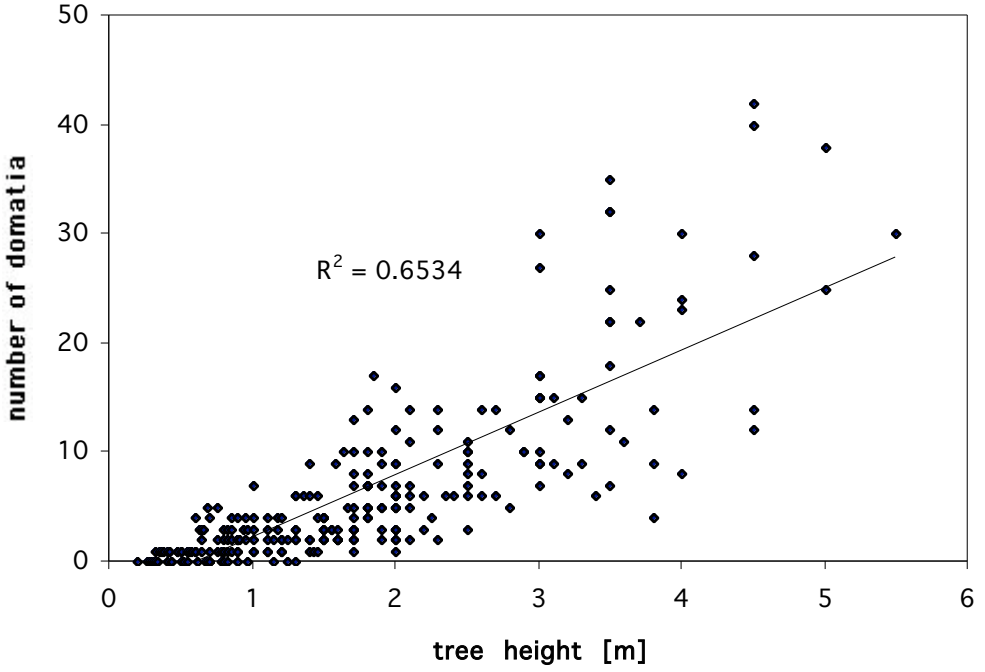


Figure 4-58: Relation between tree height and number of domatia per tree in Bornean myrmecophytic *Neonauclea* spp. (n=274). Range of trees measured: 0.2–5.5 m tall. Resprouting stumps are excluded from the analysis because they produce domatia at a seemingly lower height.

Between the Bornean and extra-Bornean myrmecophytic *Neonauclea* species I observed a general and constant difference in domatia structure (Fig. 4-59). In the former, the domatia are formed by an internode expansion containing soft white pith which has to be excavated by the ants. Pith removal by colonising ants is thus a prerequisite to utilise the domatia as nesting space. In the latter, however, the pith of the domatium dries up *prior* to ant colonisation, and the resulting cavity is used as a nest chamber (Fig. 4-59C). In all Bornean and extra-Bornean myrmecophytic *Neonauclea*, no internal connections exist between the domatia; the nesting space thus consists of separated containers distributed over the tree crown.

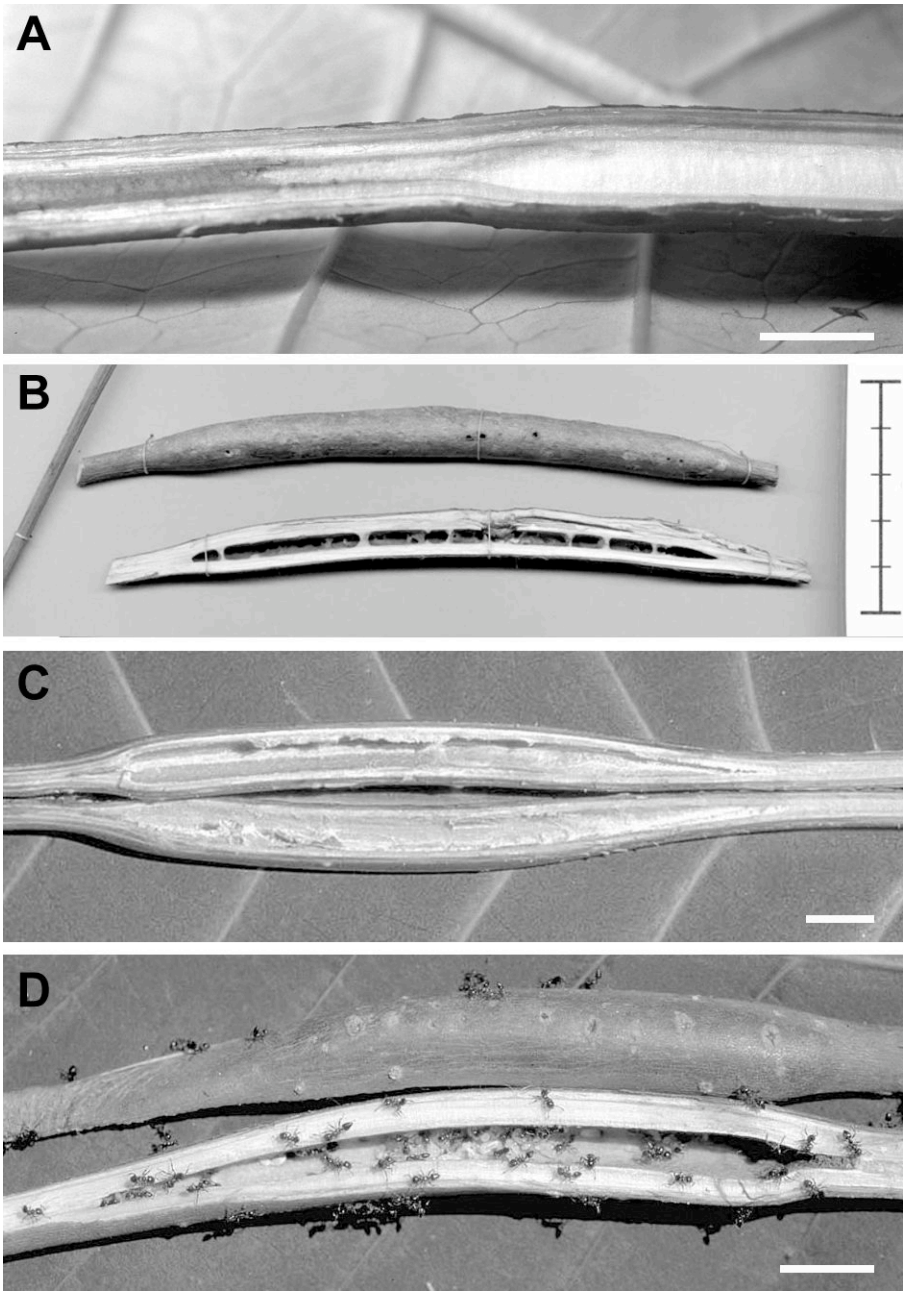


Figure 4-59: Longitudinal sections of *Neonauclea* domatia from Borneo (A-B) and Sumatra (C-D). **A**: the pith structure changes abruptly from the non-dilated to the swollen stem part. The pith becomes white and soft but does not disintegrate; **B**: by hollowing out the pith, *Cladomyrma* ants typically leave perforated pith septa which become woody, thus the domatium is partitioned into a row of connected nest chambers; **C**: young unoccupied domatium of *N. cyrtopoda* with completely disintegrated pith; **D**: *Crematogaster* ants do not have to hollow out the pith and thus inhabit a single, non-partitioned domatium chamber. Scale bars (A, C, D): 1 cm; scale bar (B): 5 cm.

Ant inhabitants: The Bornean and extra-Bornean myrmecophytic *Neonauclea* species, respectively, are inhabited by different ant genera. The formicine *Cladomyrma* species colonise the Bornean myrmecophytic *Neonauclea*. In contrast, the myrmicine *Crematogaster* species inhabit the extra-Bornean *Neonauclea* ant-

plants: species of the subgenus *Physocrema* associate with Sumatran *Neonauclea cyrtopoda* and *N. superba*, and *Decacrema* species colonise *Neonauclea* trees in Sulawesi (MASCHWITZ & FIALA 1995; own observations, n~50).

There are no indications that any extra-Bornean myrmecophytic *Neonauclea* species is inhabited by *Cladomyrma* ants. First, although *Cladomyrma* has been found on the Malay Peninsula, Sumatra and Borneo the genus has never been reported from other parts of the Malay Archipelago. Second, the two *Cladomyrma* species (*C. maschwitzi* and *C. crypteroniae*) shared between Borneo and a restricted area of Sumatra are very host-specific and neither colonise the other myrmecophytic *Neonauclea* species of Borneo nor those of Sumatra. Third, in a herbarium specimen (PNH 19638) of the sole anambiguously known myrmecophytic *Neonauclea* species from the Philippines, *N. formicaria*, I recovered *Crematogaster* ants from its domatia. This ant genus has also been reported as occupant of *N. formicaria* by BEQUAERT (1922; p. 528). Fourth, Sulawesian *Neonauclea* ant-plants have been shown by MASCHWITZ & FIALA (1995) to regularly harbour *Crematogaster* ants. This taxon was also sampled by QUEK et al. (2004) from *Neonauclea* domatia in Sulawesi. Fifth, domatia structure differs between *Cladomyrma*- and *Crematogaster*-occupied *Neonauclea* species (see above). According to the examination of extensive herbarium material, all extra-Bornean myrmecophytic *Neonauclea* possess a domatia type indicative of *Crematogaster* inhabitation. Taken together, these observations speak strongly for a clear disparity of *Neonauclea* ant association. Whereas Bornean *Neonauclea* ant-plants are regularly associated with *Cladomyrma* ants, the extra-Bornean *Neonauclea* species associate with *Crematogaster* ants.

The primary colonisers of all Bornean *Neonauclea* ant-plant species are four species of *Cladomyrma* ants, *C. aurochaetae*, *C. dianeae*, *C. hewitti*, and *C. maryatiae*, all belonging to the 'raised petiole group' (AGOSTI, MOOG & MASCHWITZ 1999). Among *Cladomyrma*, *C. dianeae* appears to be the most common inhabitant. I have collected colonies of this species from *N. borneensis*, *N. gigantea*, *N. longipedunculata*, *N*. sp. C and E, and probably *N. paracyrtopoda*. *C. dianeae* has also been sampled by DIANE DAVIDSON from three *Neonauclea* host plants (sp. #1, #2 and #3) but their species identity could not be established. *C. aurochaetae* is known from *N. gigantea*, *C. hewitti* from both *N. longipedunculata* and *N. pseudocalycina*, and *C. maryatiae* from *Neonauclea* species C and D (own collections), resp. sp. #2 of DIANE DAVIDSON. Our knowledge of these host affiliations will be enhanced by a deeper understanding of *Neonauclea* taxonomy and by sampling over a larger geographical scale.

Although the predominant coloniser of Bornean *Neonauclea* is *Cladomyrma* (see below), several other ant species from different genera (e.g., *Camponotus*, *Crematogaster*, *Philidris*, *Technomyrmex*) were occasionally observed to inhabit *Neonauclea* domatia. These arboreal species merely take possession of domatia excavated and abandoned by *Cladomyrma* ants (secondary colonisation), and they usually occupy the most basal (sometimes dead) domatia of a tree. The factors that may be responsible for the absence or eviction of *Cladomyrma* in certain *Neonauclea* populations will be presented below (Ant occupancy rate, p. 117).

Onset of ant occupancy: In areas where a healthy *Cladomyrma* population is established, each *Neonauclea* sapling having produced its first domatium is colonised by foundress queens as soon as the domatium reaches its full length. Occupancy rate of domatia-bearing saplings of the size class 0.32 to 1.0 m height was close to 75% (61 of n=82 plants). Multiple colonisations of a single domatium are the rule, usually each queen inhabits a separate chamber (Fig. 4-60). Up to 7 founding chambers may be 'squeezed' into a domatium but, on average, about 2 to 3 chambers per domatium are found (Fig. 4-61).

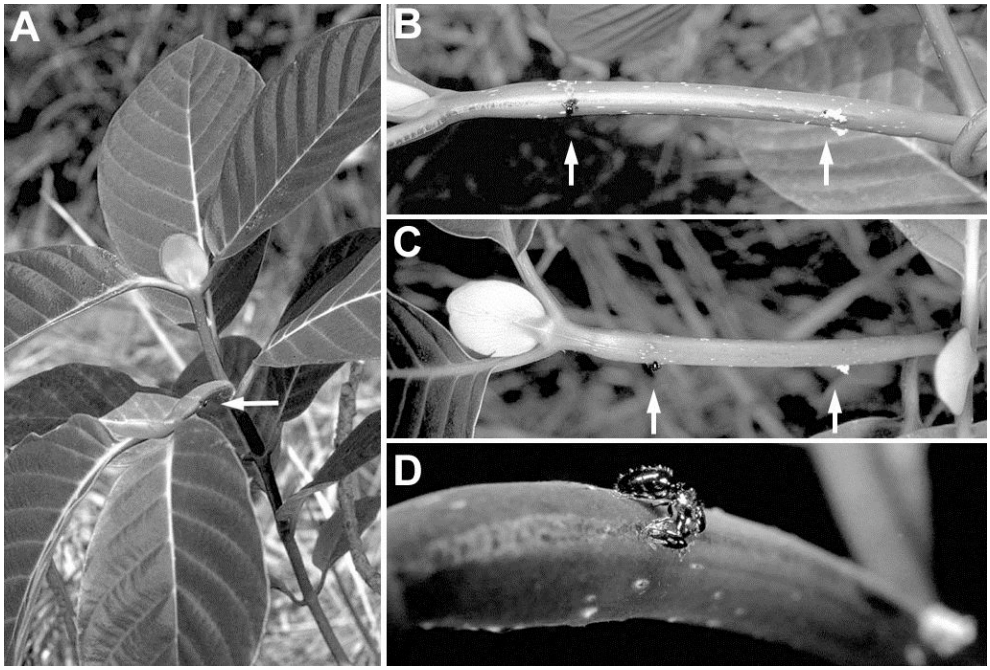


Figure 4-60: *Neonauclea gigantea* with founding queens of *Cladomyrma* entering a domatium. Arrows indicate point of entries. **A**: sapling with newly developed domatium (directed towards the observer); **B**: lateral view of domatium (approx. 12 cm long) with two foundations: a queen in the process of chewing an entrance hole (left) and pith remains at an entrance hole where the foundress already entered the hollowed-out chamber (right) ; **C**: top view of B; **D**: detail of B and C; the dealate foundress gnaws a hole into the prostoma line running along the side of the domatium.

It is noteworthy that foundress queens arriving later at an already occupied domatium appear to avoid pre-existing chambers and chew their chamber in the non-occupied section of the domatium while paying attention not to fuse their own chamber with that of the neighbouring foundress. In case the remaining non-occupied section of a domatium is small, the chamber of the late arriving queen will be small as well. The walls separating the founding chambers of a domatium have a charcacteristic which is important to the foundresses living within them. During the founding stage, the pith of the domatium undergoes a significant change in its texture. The interior walls at each end of a founding chamber which initially consist of soft pith become sclerotized shortly after founding took place (Fig. 4-61). If the hardening of the pithy walls is, for example, due to contact with atmospheric air or triggered by secretions of the foundress ant remains to be tested. Whatever the cause, the hard walls certainly help in keeping founding queens within a single domatium apart from each other.

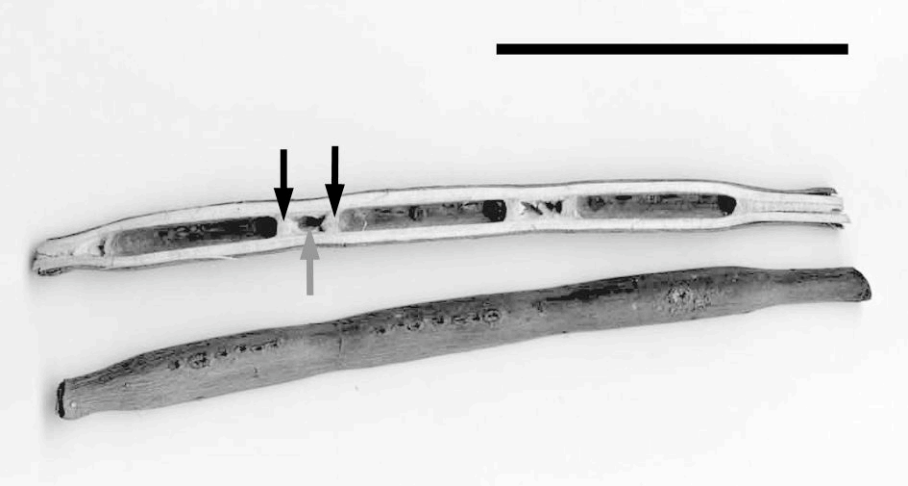


Figure 4-61: Longitudinal section of a domatium of *Neonauclea gigantea* with 3 founding chambers of *Cladomyrma dianeae* (from herbarium specimen AMO-019, Poring Hot Springs, Sabah, Borneo; leg. J. Moog). The pithy walls at each end of a founding chamber become woody and hard (black arrows) whereas the pith between the hardend walls remains soft (grey arrow; dried up in dissected herbarium specimens). Note the constriction of the domatium diameter between founding chambers. Scale bar: 5 cm.

Domatia colonised by several foundress ants often have their outer diameter constricted between each chamber (Fig. 4-61). Superficially, this suggests that the founding queens excert a physically or chemically mediated force on the volume of their abode. For example, the swelling of a domatium may be accelerated in response to mechanical stimuli such as the drilling of holes and the removal of pith by an ant foundress. Such a reaction to wounding has been demonstrated in the facultative neotropical ant-plant *Vochysia vismiaefolia* (BLÜTHGEN & WESENBERG 2001). However, if a domatium is colonised prior to its final stage of hypertrophy (which often appears

to be the case), the hardened pith walls between chambers may hinder the further expansion of the domatium in these sections. At present, the origin of the conspicuous irregularities in the outer diameter of *Neonauclea* domatia is unknown.

After a colony is established on a plant, a fairly constant relationship between colony size and the total number of domatia –rather than to tree height– exists (linear regression, $R^2 = 0.928$ and $R^2 = 0.680$, respectively; Fig. 4-62).

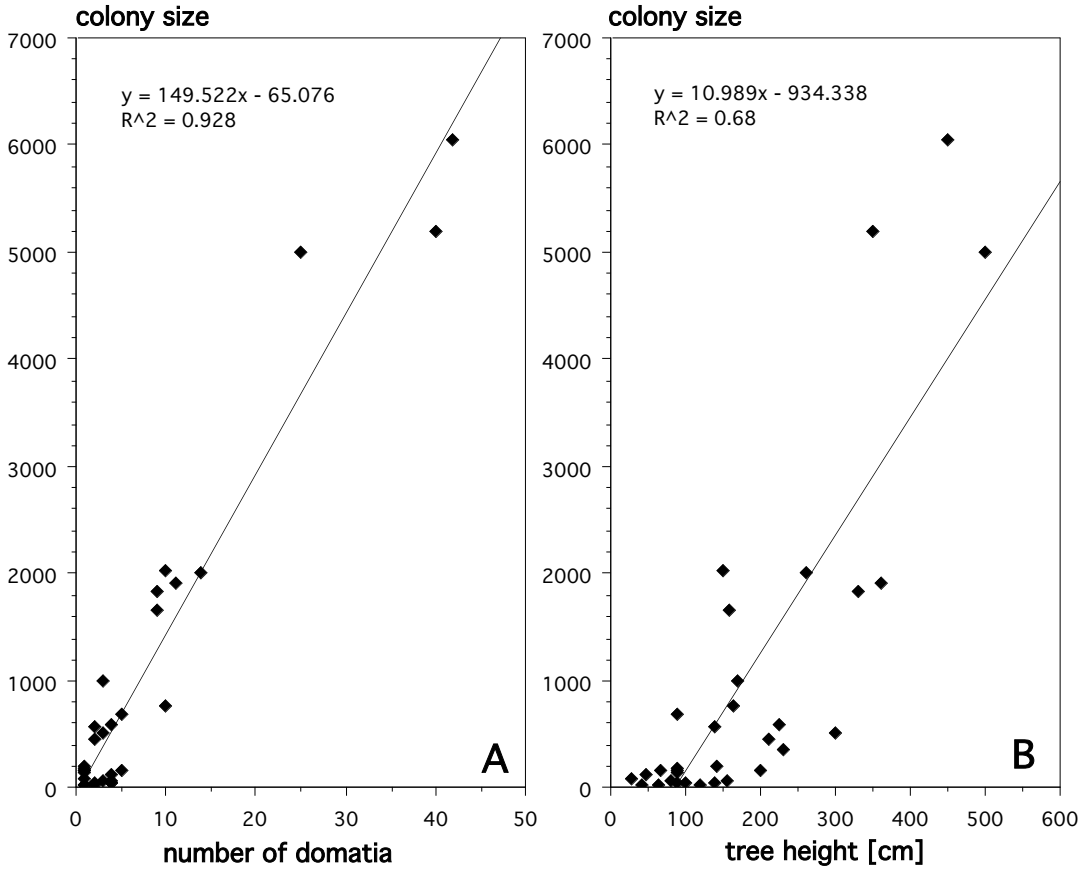


Figure 4-62: Colony size (number of workers) of *Cladomyrma* spp. in relation to the total number of domatia per tree (**A**) and tree height (**B**) in Bornean *Neonauclea* ant-plants. Included are plants bearing at least one domatium: $n_A = 31$; $n_B = 32$.

The nesting space of a *Cladomyrma* colony is usually restricted to the total domatia space offered by a single *Neonauclea* host plant. In very few cases, however, the ant colony extended the available nesting space (i) by hollowing out the comparatively hard pith canal of unswollen stem sections adjacent to the domatia for several centimetres, and/or (ii) by secondarily colonising neighbouring *Neonauclea* plants that are in physical contact with the initial host.

Ant occupancy rate: Of all trees censused bearing at least one domatium (n=579), 61.5% were exclusively occupied by *Cladomyrma* ants, whilst 8.8% were jointly occupied by *Cladomyrma* and other, mostly *Crematogaster* ants (Fig. 4-63). Colonies of *Crematogaster* spp. (or other non-*Cladomyrma* ants) in jointly occupied trees were usually smaller than the resident *Cladomyrma* colony and they mostly inhabited the basal or dead domatia of a tree. About one tenth (10.2%) harboured only non-*Cladomyrma* ants, and one fifth (19.5%) lacked ant occupants.

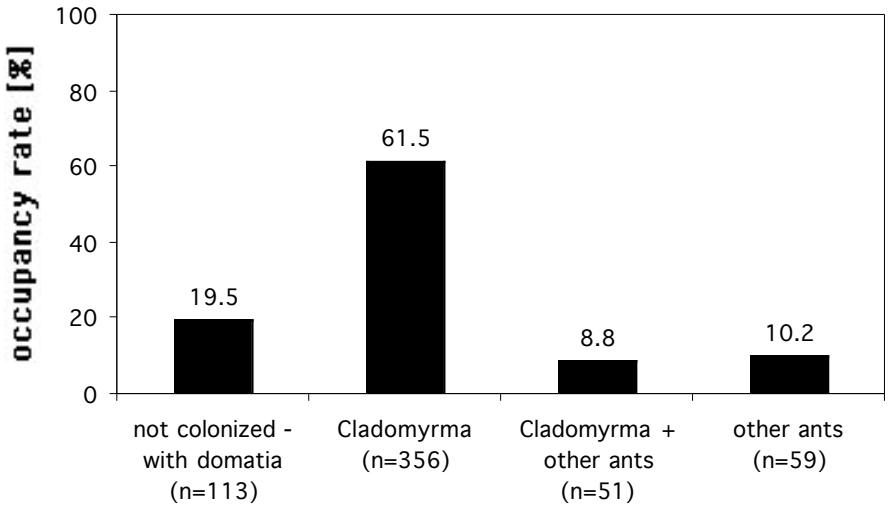


Figure 4-63: Percentage of *Neonauclea* spp occupied by *Cladomyrma* spp. and other ant species (mainly of the genus *Crematogaster*) in solely and jointly occupied trees (n=579). Included are only plants that bear at least one domatium.

Relative abundances of *Cladomyrma* and non-*Cladomyrma* ant species on trees differed from one another and varied with tree height. Whereas occupancy rate of *Cladomyrma* was fairly constant across all size classes (Fig. 4-64), trees exclusively inhabited by non-*Cladomyrma* ants (predominantly *Crematogaster* spp.) were significantly taller than trees exclusively occupied by *Cladomyrma* ants (median 3.25 m and 2.0 m in height, respectively; Mann-Whitney U-test: $P = 0.0005$; Fig. 4-65). In contrast, trees solely occupied by *Cladomyrma* were not significantly different in height from trees jointly occupied by *Cladomyrma* and other ants (U-test, $P = 0.17$). As is to be expected, the proportion of unoccupied trees decreases with tree height but increases in the biggest size class almost to the level of the smallest (Fig. 4-64).

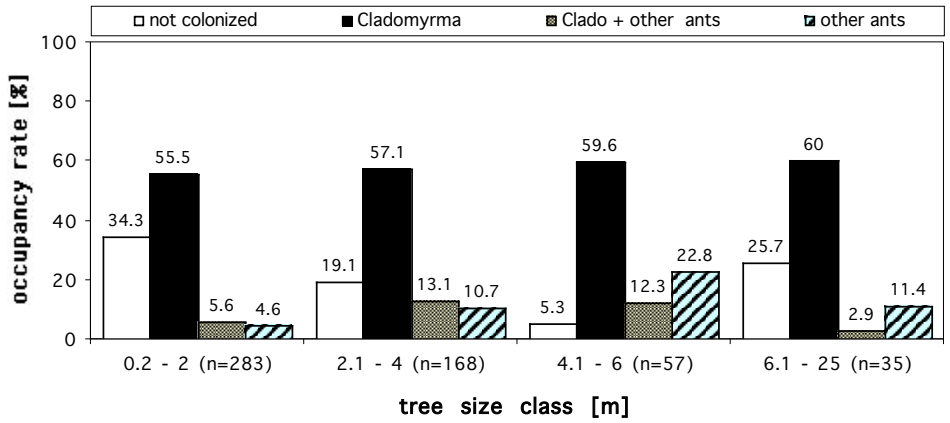


Figure 4-64: Ant occupancy rate of *Neonauclea* spp. in relation to tree height (n=543). The smallest size class (0.2 to 2 m) includes 36 plants having not yet developed a domatium. If these are excluded, proportion of *Cladomyrma*-occupied plants for the smallest size class is 63.5%.

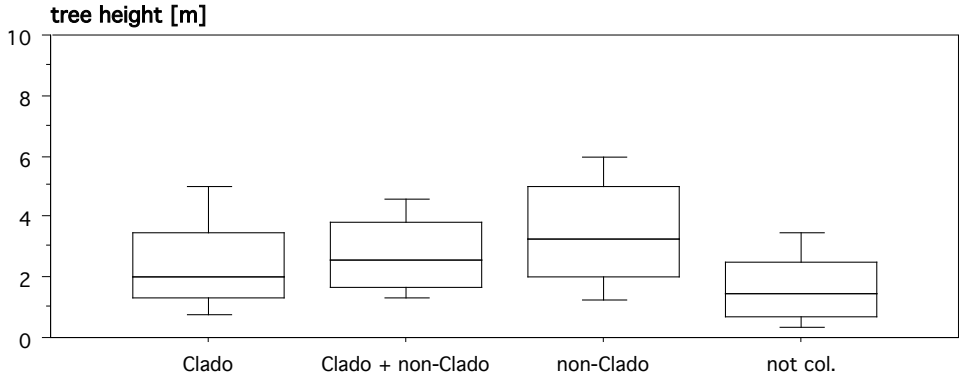


Figure 4-65: Height of *Neonauclea* trees in relation to ant occupant (n=543). Trees exclusively occupied by *Cladomyrma* spp. (n=308) differed significantly in height from trees solely inhabited by non-*Cladomyrma* ants (n=48; Mann-Whitney U-test, P = 0.0005) but difference in height to trees jointly occupied by *Cladomyrma* + non-*Cladomyrma* ants (n=46) was not significant (*P* = 0.17). [For explanation of box-whisker plots see figure 4-45.]

Several factors, including disturbance regime, forest type, elevation and interspecific competition, influence the distribution of *Cladomyrma* on *Neonauclea* trees. Generally, *Neonauclea* species tend to occur in areas of (frequent) disturbance which are embedded in primary and secondary forest, e.g., river margins, landslides, new roadcuts or new clearings in otherwise forested areas. The ecological amplitude of *Neonauclea gigantea* is probably the most variable of all *Neonauclea* species; it grows as "forest" species in small areas of natural disturbances such as forest gaps but it also can invade large man-made disturbances, sometimes dominating on frequently

chopped roadsides and agricultural land. *Neonauclea* trees growing in the latter habitats have similar levels of occupancy by *Cladomyrma* as those of forested habitats as long as these habitats are in proximity to forests. However, the proportion of *Cladomyrma*-occupied trees drops quickly with increasing distance to forest sources. Occupancy rate of *Neonauclea* spp. in relation to habitat is presented in figure 4-66. It immediately becomes apparent that the average proportion of trees occupied by *Cladomyrma* increases with the proximity to forested habitats. This relationship is probably caused by factors which all act in concert. For example, the competition of *Cladomyrma* with *Crematogaster* ants appears to increase in areas of strong disturbance. In habitat A (Fig. 4-66) the proportion of trees solely occupied by alien ants was 13.1% (n=55) of which at least one half (n=28) showed signs of former *Cladomyrma* inhabitation (indicated by the type of entrance holes or remains of *Cladomyrma* workers).

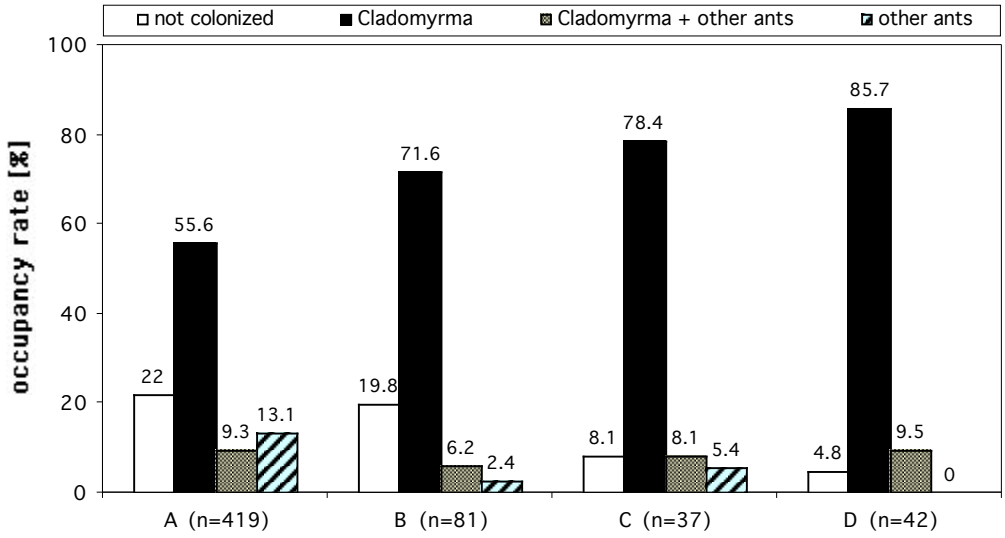


Figure 4-66: Ant occupancy rate of *Neonauclea* spp. in relation to habitat (n=579). A=strongly disturbed road side vegetation; B=disturbed, secondary growth; C=forest fringes; D=forest.

In the field I observed that certain *Crematogaster* species, which proliferate principally by the expansion of existing colonies, can invade a *Cladomyrma*-occupied *Neonauclea* tree and actively evict the resident colony. For example, I found a small *Neonauclea gigantea* tree whose *Cladomyrma* colony was engaged in a fierce battle against an invading *Crematogaster* colony. The resident colony had already lost three of the total four domatia but still maintained the last domatium in which the remaining *Cladomyrma* workers assembled around the queen. About 200 *Crematogaster* workers covered the exterior of the domatium and at each of the entrance holes

workers tried to enter the domatium. Some workers were observed to gnaw on the hole margins, apparently trying to enlarge the hole diameter. Several *Crematogaster* workers staggered helplessly along the domatium, they were propably hit by formic acid released by the defending *Cladomyrma* workers. During the whole afternoon the battle continued and the *Crematogaster* ants apparently did not make any progress. I assume that the fight between *Cladomyrma* and *Crematogaster* had already lasted for several days since the *Crematogaster* workers had established new aggregations of trophobiotic mealybugs in the axils of the leaf petioles. Such trophobiotic sites on the plant surface are never maintaind by *Cladomyrma* ants and, therefore, the aggregations of trophobionts tended by *Crematogaster* do not simply represent a takeover of trophobiotic sites abandoned by *Cladomyrma*.

In highly disturbed study sites, vacant *Neonauclea* trees are relatively common (Fig. 4-66), and a considerable portion of these empty trees is presumably created by predators of ants and their brood. At these sites, many trees had domatia torn open by predators, and the conspicuous damages always occurred on previously ant-inhabited domatia, often founding chambers of *Cladomyrma*. In a monospecific stand of *Neonauclea gigantea* at a highly disturbed site surrounded by agricultural land, 50.4% of all trees (n=226) possessed at least one domatium torn open by a predator. The major predators are probably squirrels of the genus *Callosciurus*. The tooth marks and damages were very similar to those observed in *Macaranga* ant-plants attacked by *Callosciurus notatus* (FEDERLE et al. 1999). In Sabah (Borneo), Tina Urschek and I observed on two occasions a *C. notatus* squirrel inspecting the domatia of *N. gigantea* trees. The squirrel moved from twig to twig and stopped at each domatium, assumably checking for ant inhabitants. However, we could not observe the opening of the domatia itself because the later inspection revealed that these domatia –although previously occupied by ants– were now empty. These observations suggest that repeated catastrophic damage to the domatia, destroying foundings or the occupying *Cladomyrma* colony, create empty *Neonauclea* trees that are targets for colony initiation by specialist *Cladomyrma* or colony expansion by generalist *Crematogaster* ants living in the surrounding vegetation. This, in turn, likely leads to a high turn over of ant occupancy, interspersed by periods of vacancies.

In addition to disturbance regime other habitat features such as temperature and rainfall probably influence the distribution of the *Cladomyrma-Neonauclea* association. The upper elevational limit for *Cladomyrma* may be determined by cold, wet conditions. At altitudes of about 1250–1300 m a.s.l. the abundance of *Cladomyrma* species inhabiting *Neonauclea* dropped quickly and above 1350 m *Cladomyrma* has never been found (Fig. 4-67). In elevational transects, *Neonauclea* ant-plants far

exceed their *Cladomyrma* ant partners. For example, *Neonauclea gigantea* has been found in montane forests of the Kinabalu NP (Sabah) at elevations of 1650 m. Montane populations of myrmecophytic *Neonauclea* still produce domatia in the absence of their specific ant partners, however, even generalist arboreal ants with high elevation tolerance do not colonise the vacant domatia (Fig. 4-67), assumably because they lack the ability to chew their access into the internode interior.

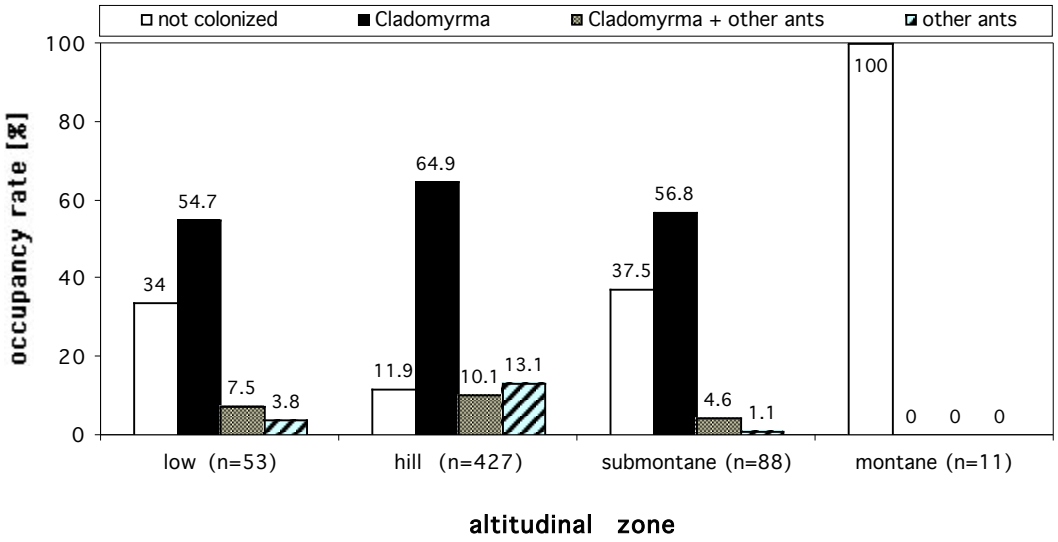


Figure 4-67: Ant occupancy rate of *Neonauclea* spp. in relation to altitude: low=0-300m; hill=300–800m; submontane=800–1350m; montane=1350–2000m

Herbarium study: Material was systematically examined from 238 different collections of all 17 Bornean *Neonauclea* species reported to possess ant-domatia (RIDSDALE 1989). Presence of swollen internodes could be easily determined and the result was consistent with that established by RIDSDALE (1989). Tables 4-3 and 4-4 list, for each species, the proportion of collections bearing domatia and several parameters such as domatia length, domatia diameter, and their respective proportion relative to the internode's total length and unswollen diameter.

Specimens of some species, especially those from Sulawesi, all bear domatia (Tab. 4-3). However, the rather low percentage of other specimens exhibiting domatia (e.g., 26% for *N. gigantea* and 42% for *N. excelsioides*) seems to indicate that domatia production is not a constant character in species. However, botanists usually collect the terminal parts of a branch which bears the flowering and fruiting heads and omit the more proximal domatia, particularly when leaf sizes and domatia are large. [Sulawesian species tend to have smaller leaves and less robust branches and more

collected material can thus be mounted onto a herbarium sheet.] Furthermore, my field studies revealed that, for example, *Neonauclea gigantea*, constantly produces domatia even in areas where the ant partner is absent. In addition, my herbar survey showed that domatia production occurs throughout the distribution of each *Neonauclea* species. Thus, domatia appear to be a constant and reliable character for all *Neonauclea* ant-plant species.

Table 4-3: Proportion of herbarium collections bearing swollen internodes of 17 *Neonauclea* species reported to produce ant-domatia (RIDSDALE 1989); coll. with domatia: a single collection, often distributed over several herbaria, may bear more than one domatium (= total no.); region: B = Borneo, PH = Philippines, SL = Sulawesi, SU = Sumatra.

Neonauclea taxon	*n*	coll. with domatia (total no.)	%	geographic region
artocarpoides	20	12 (13)	60	B
borneensis	14	10 (13)	71	B
butonensis	1	1	100	SL
calcarea	14	7 (9)	50	B
celebica	15	11 (23)	73	SL
cyrtopoda	18	15 (26)	83	SU
excelsioides	12	5 (8)	42	B
formicaria	18	10	56	PH
gigantea	46	12	26	B
havilandii	11	9 (20)	82	SL
longipedunculata	31	14 (16)	45	B
paracyrtopoda	8	5	62	B
pseudocalycina	12	6 (10)	50	B
rupestris	1	1 (2)	100	SL
superba	8	5 (7)	63	SU
unicapitulifera	6	6 (11)	100	SL
ventricosa	3	3 (6)	100	SL

It remains to be verified whether populations of *Neonauclea* myrmecophytes loose their ant domiciles in marginal areas of their distribution. Progressive loss of ant-related traits is, for example, known from the neotropical ant-plant *Cecropia peltata* occurring outside its natural distribution (JANZEN 1973, RICKSON 1977, MCKEY 1988b, PUTZ & HOLBROOK 1988).

According to herbar collections and own field sampling, length of domatia and other domatia parameters (Tab. 4-4) were highly variable between and within species. Field observations suggest that domatia length may also vary at the intra-individual level.

Saplings appear to produce longer domatia than mature, flowering trees and distal domatia are shorter than proximal ones. These variations are probably not adequately represented in the data obtained from herbarium specimens (Tab. 4-4), because the domatia are usually collected from distal branches near flowering heads from reproductive trees. Despite these sources of variation some species seem to differ from the remaining species, i.e., *N. gigantea* has the largest, *N. artocarpoides, N. excelsioides* and *N. calcarea* the shortest domatia.

Table 4-4: Domatia size parameters of 17 myrmecophytic *Neonauclea* species, measured from dried specimens of herbarium material. For *gigantea*, *paracyrtopoda* and *pseudocalycina* data from dried material of my own collections are added. In many cases the relative length of a domatium to the total length of an internode could not be obtained because internodes were not collected in its entireness. The increase of internode diameter was calculated from the width of domatia (measured across the lateral prostoma sides because they are little affected by secondary growth) and the smallest diameter of the ± round unswollen internode section distal of the domatium. Missing data (–): not measured. Grey rows denote *Neonauclea* species predominantly inhabited by *Cladomyrma*; the remaining species have ant associates of the genus *Crematogaster* ([1] = subg. *Decacrema*, [2] = subg. *Physocrema*; [3] = subg. not established).

Neonauclea taxon	mean domatium length [mm] (range; *n*)	mean proportion of total internode length [%] (range; *n*)	mean domatium diameter [mm] (range; *n*)	mean increase in diameter [%] (range; *n*)
artocarpoides	**39** (25–80; *13*)	**34** (30–38; *4*)	**8.4** (5.0–11.0; *8*)	**97** (60–144; *6*)
borneensis	**51** (26–70; *13*)	**47** (32–59; *6*)	**9.2** (9.0–11.0; *5*)	**85** (57–100; *5*)
butonensis [1]	**37** (37; *1*)	**41** (41; *1*)	–	–
calcarea	**39** (26–79; *9*)	**50** (44–59; *3*)	**9.3** (7.0–12.0; *5*)	**103** (100–112; *4*)
celebica [1]	**41** (25–61; *23*)	**37** (17–51; *19*)	**4.8** (4.0–6.0; *9*)	–
cyrtopoda [2]	**56** (36–92; *26*)	**43** (30–47; *21*)	**12.4** (8.0–15.0; *12*)	**117** (78–155;*8*)
excelsioides	**34** (29–48; *8*)	**27** (26–27; *2*)	**9.8** (8.0–11.0; *4*)	**164** (142–175; *3*)
formicaria [3]	**53** (39–58; *10*)	**53** (53; *1*)	**8.0** (8.0; *1*)	–
gigantea	**89** (40–250; *27*)	**64** (60–71; *6*)	**9.9** (7.5–12.0; *15*)	**90** (33–134; *5*)
havilandii [1]	**36** (22–65; *20*)	**32** (25–41; *15*)	**7.8** (7.0–9.0; *8*)	**129** (129; *1*)
longipedunculata	**56** (26–87; *17*)	**39** (25–51; *5*)	**9.8** (7.2–17.0; *15*)	**110** (100–125; *5*)
paracyrtopoda	**72** (33–130; *13*)	**35** (32–37; *2*)	**9.7** (7.8–12.5; *10*)	**80** (60–100; *2*)
pseudocalycina	**66** (32–105; *24*)	**44** (35–52; *2*)	**8.6** (5.5–14.0; *17*)	**79** (33–128; *6*)
rupestris [1]	**52** (48–55; *2*)	–	–	–
superba [2]	**55** (31–67; *7*)	**39** 30–47; *5*)	**12.0** (8.0–17.0; *4*)	–
unicapitulifera [1]	**42** (29–59; *11*)	**30** (23–38; *7*)	**6.0** (5.0–8.0; *5*)	–
ventricosa [1]	**79** (58–104; *6*)	**63** (52–69; *4*)	**6.8** (6.0–8.0; *6*)	–

Domatium length, however, is not a sufficient indicator of domatium volume and hence available nesting space. This becomes apparent when domatium diameter is compared. Some Bornean *Neonauclea* have short domatia but their diameter is distinctly enlarged relative to Sulawesian species (Tab. 4-5). In comparison to Sulawesian *Neonauclea* species, those from Borneo and Sumatra generally tend to have more robust branches and domatia. Sulawesian species also differ from the remaining species by the relatively small proportion the domatium occupies of the full internode length (Tab. 4-5).

Table 4-5: Domatium size parameters of myrmecophytic *Neonauclea* grouped according to the geographic region which corresponds with the respective ant partner. Data from Sumatran and Sulawesian *Neonauclea*, inhabited by *Crematogaster* (subgenera *Physocrema* and *Decacrema*) are also combined in the group extra-Borneo. The groups were statistically compared using the non-parametric Mann-Whitney U-test.

myrmecophytic *Neonauclea* geographic region (ant partner)	domatium length [mm] mean ± SD (range; *n*)	proportion of total internode length [%] mean ± SD (range; *n*)	domatium diameter [mm] mean ± SD (range; *n*)	increase in diameter [%] mean ± SD (range; *n*)
Borneo (*Cladomyrma*)	62.1 ± 33.1 (25–250; *122*)	45 ± 13.6 (25–71; *30*)	9.4 ± 2.1 (4.0–17.0; *78*)	98 ± 33.8 (33–175; *36*)
Sumatra (*Physocrema*)	55.5 ± 14.4 (31–92; *33*)	42 ± 4.9 (30–47; *26*)	12.3 ± 2.6 (8.0–17.0; *16*)	117 ± 25.8 (78–155; *8*)
Sulawesi (*Decacrema*)	43.6 ± 15.7 (22–104; *63*)	37 ± 11.2 (17–69; *46*)	6.3 ± 1.4 (4.0–9.0; *28*)	129 (129; *1*)
extra-Borneo: Sumatra, Sulawesi	47.7 ± 16.2 (22–104; *96*)	39 ± 9.7 (17–69; *72*)	8.5 ± 3.5 (4.0–17.0; *44*)	118 ± 24.4 (78–155; *9*)
comparison:				
Borneo / Sumatra	P = 0.8732	P = 0.5164	**P < 0.0001 *** **	P = 0.0884
Borneo / Sulawesi	**P < 0.0001 *** **	**P = 0.0081 ** **	**P < 0.0001 *** **	–
Sumatra / Sulawesi	**P < 0.0001 *** **	**P = 0.0012 ** **	**P < 0.0001 *** **	–
Borneo / extra-Borneo	**P = 0.0021 ** **	**P = 0.0341 * **	**P = 0.0118 * **	P = 0.0555

The statistical comparison of each measured domatium parameter (Tab. 4-5) suggests that the grouping according to the geographical region (and hence ant partner) is, at least in part, reflected in domatium characteristics. On average, Bornean species have longer (62.1 mm) and thicker domatia (9.4 mm) than extra-Bornean species (47.7 and 8.5 mm, respectively), but stouter domatia are not the result of an increased swelling –which is actually the lowest (98%)– but of a generally larger stem diameter. The significant differences in three measured parameters between Bornean and extra-Bornean species are caused by the Sulawesian group which differs highly and significantly from both the Bornean and Sumatran species.

The results on domatia parameters obtained from a rather low sample that probably underestimates the variation seen in the field must be considered preliminary, and more data are needed to assess if the observed differences among groups of geographical disjunct *Neonauclea* species can be confirmed.

In most domatia-bearing herbarium collections of *Neonauclea* ant entrance holes were evident. Nevertheless, ant inhabitation was rarely mentioned by collectors:

1.) *N. artocarpoides*: BEAMAN 8582, "Ants in hollow stem."
2.) *N. cyrtopoda*: LÖRZING 4203, "Very typical are galls, caused by long, spiral threads (a mould?). The hollow branch galls are inhabited by ants" (translated from dutch). The specimen shows typical domatia, not galls (pers. observation); STOMPS no. ?, “Mierenplant“, (dutch, translation: ant-plant); DE VOGEL 2537, “Twigs inhabited by ants“; DE WILDE 14840, “Twigs here and there with swellings inhabited by ants“; DE WILDE 19238, “Hollow twig parts inhabited by ants“; YL 3626, leg. Y. LAUMONIER, “Myrmecophily of the twigs“; YL 6936, leg. Y. LAUMONIER, “Associated with ants which have an erected abdomen while walking.“
3.) *N. excelsioides*: CER 2451, leg. C. E. RIDSDALE, "Myrmedomes present."
4.) *N. gigantea*: TFB 1295, "Stem inhabited by ants"; WINKLER 2924, "An den Zweigen treten etwa 25 cm lange Ameisenzellen auf" (german, translation: the twigs bear about 25 cm long ant cells).
5.) *N. havilandii*: KOORDERS 18632/3, "Es finden sich hier von Ameisen bewohnte Hohlräume in den aufgetrieben Stengeln in der Nähe der Blüthen“ (german, translation: there are hollow cavities, inhabited by ants, in the fistulose stems near the flowers).
6.) *N. longipedunculata*: WKM 328, leg. WONG KHOON MENG, "Twigs ant-inhabited"; WKM 2280, leg. WONG KHOON MENG, "Twigs swollen in places, ant-inhabited."
7.) *N. paracyrtopoda*: 900821-1/3, leg. PUFF, IGERSHEIM & MARTINELLO, "Ant-plant: swollen internodes".

Note on species identification: The taxonomy of *Neonauclea* Merr. has been problematic since tropical exploration increased in the 19th and 20th Centuries. Despite the attention of many notable botanists (HAVILAND 1897, ELMER 1911, MERRILL 1915, MERRILL & PERRY 1944), the taxonomy of *Neonauclea* remained difficult. More recently, RIDSDALE'S work (1978, 1989) has aided in clarifying the taxonomy of *Neonauclea*. RIDSDALE (1989) based his revision of *Neonauclea* mainly on the very characteristic calyx lobes which overtop and conceal the young corollas (Fig. 4-68). Commonly, the expansion of the corollas pushes upward the apical portion of the calyx lobes, ultimately breaking their shaft. Remnants of the upper part of the calyx lobes are thus often found between corollas in old flowering heads and rarely even in fruiting heads. The apical portions of the calyx lobes and mature flowering heads are required to identify species with certainty. Fruting material alone is difficult or impossible to identify.

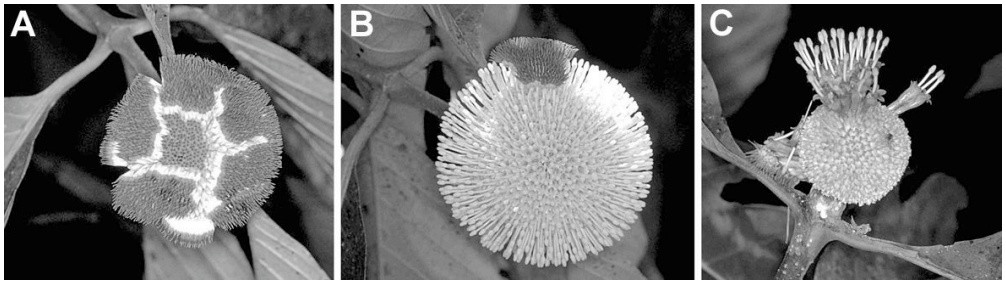


Figure 4-68: Developmental stages of the flowering head of Sumatran *Neonauclea cyrtopoda*. **A**: immature flowering head covered by the accrescent calyx lobes which detach in a mass by the expansion of the numerous corollas; **B**: young flowering head with expanded corollas and styles crowned by remnants of accrescent calyx lobes; **C**: old flowering head with few corollas remaining on the spherical receptacle. Scale: diameter of flowering head (B) across corollas about 6–7 cm.

RIDSDALE'S revision is an important improvement of previous treatments of the genus, although I realised during my herbarium studies that the calyx summits, considered characteristic for many species, are sometimes more variable than recognised by RIDSDALE (1989). This variation was evident both at the species and individual level (e.g., BECCARI 1890, BRUN 762, CLEMENS 26965, SAN 23141, SAN 79888), making the identification of some of my collections particularly difficult. Furthermore, the *Neonauclea* ant-plants found in the field were mostly young and sterile. As the determination keys for *Neonauclea* species (RIDSDALE 1989) are primarily based on floral characters, I was often unable to identify these collections. Stipules belong to the few vegetative characters that may be useful for species identification but they are either unknown in some species (e.g., *Neonauclea artocarpoides* and *N. calcarea*) or their intraspecific range of variation in size and shape is uncertain.

Unfortunately, holotype specimens of *Neonauclea excelsioides*, *N. paracyrtopoda* and *N. pseudocalycina* have been lost in 1998. Herbarium sheets in Leiden mounted with photostatic copies of the missing specimens carried a label note by C. E. RIDSDALE: “Boat carrying a loan of 3 postal packages of Naucleeae sunk in the Azores, including this specimen“. Although I could examine the holotypes before they were lost I could not re-examine the variation of certain flower and leaf characters during my next visit to the Rijksherbarium in Leiden.

Species account of Bornean myrmecophytic Neonauclea

Neonauclea artocarpoides Ridsdale

Figure 4-69A

Tree up to 25 m. Habitat (according to label information of herbarium material): primary and secondary forest, riverside, pipeline track, low hills to steep hillside, and limestone; lowlands up to ca. 1000 m altitude. Distribution: Borneo (Brunei, northern Kalimantan, Sabah and northern Sarawak). Note: None of the sterile *Neonauclea* specimens collected in the field could be assigned to *N. artocarpoides* with certainty. The domatia of *N. artocarpoides* examined in herbarium material, however, possessed entrance holes identical to those of *Neonauclea* species inhabited by *Cladomyrma* ants.

Neonauclea borneensis Ridsdale

Figure 4-69B

Tree up to 12 m. Habitat (according to both herbarium information and field observations): secondary forest, roadside, and riverside; lowlands up to ca. 500 m altitude. Distribution: Borneo (Brunei, Sarawak, central Kalimantan). Note: I found the species at several locations in Sarawak (Hose Mountains, Kubah Park near Kuching, and occasionally along the Lundu-Bau road). In all cases the domatia were inhabited by *Cladomyrma dianeae* or an unidentified *Cladomyrma* species.

Neonauclea calcarea Ridsdale

Figure 4-69C

Small tree up to 10 m. Habitat (according to herbarium information): apparently restricted to forest on limestone; lowlands up to 750 m altitude. Distribution: Borneo (Sarawak). Note: Ant entrance holes in domatia of herbarium specimens of *N. calcarea* resemble those observed in *Neonauclea* species inhabited by *Cladomyrma* ants. One specimen (S.20910) examined at Kew herbarium had so-called 'secondary holes' (see p. 117, Fig. 6-1E), a character that is indicative of a *Cladomyrma* founding chamber.

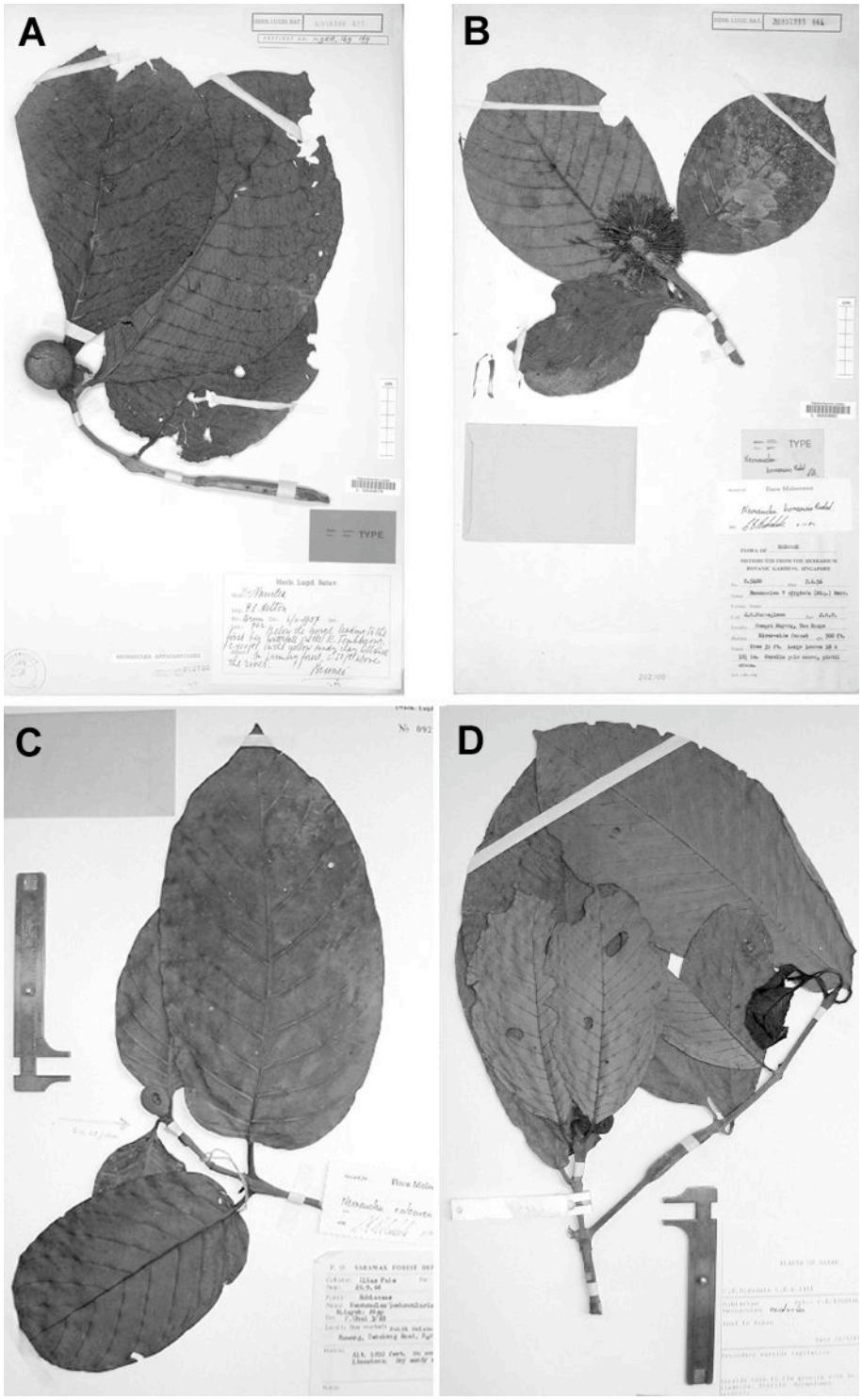


Figure 4-69: Dried specimens of myrmecophytic Bornean *Neonauclea* spp. **A**: *artocarpoides*, Type, BRUN762, Temburong, Brunei, leg. P. S. ASHTON; **B**: *borneensis*, Type, P5400, Tau Range, Sarawak, leg. J. W. PURSEGLOVE; **C**: *calcarea,* S.28067, Bukit Selabor, Serian, Sarawak; **D**: *excelsioides*, CER2451, Sukau road, Sabah, leg. C. E. RIDSDALE. A-B: scale bar: 5 cm; source: http://www.nationaalherbarium.nl; C-D: calliper rule set to 1 cm.

Neonauclea excelsioides Ridsdale

Figure 4-69D

Tree up to 30 m. Habitat (according to herbarium information): primary forest, secondary forest, riverside, hillside, wayside in secondary vegetation, and 'working area'; lowlands. Contrary to RIDSDALE (1989), who states a possible restriction of *N. excelsioides* to limestone habitat, not a single limestone record was found in the available herbarium material. Distribution: Borneo (Sabah, Kalimantan, one collection [S.43950] from Sarawak). Note: Probably inhabited by *Cladomyrma* ants, as indicated by the entrance holes examined in domatia of herbarium material.

Neonauclea gigantea (Valeton) Merrill

Figures 4-70, 4-71, 72

Tree attaing 30 to 40 m; common, locally very abundant. Habitat: gaps and riversides in primary and secondary forest, disturbed forest, early successional vegetation, landslides, logging trails and roadsides; lowlands to ca. 1,600 m (pers. observation). Distribution: Borneo (Brunei, Kalimantan, Sabah, Sarawak). Note: *Neonauclea gigantea* is the most common and widely distributed *Neonauclea* ant-plant species with a high ecological amplitude. The species can grow both in small gaps of pristine forests but is also adapted to heavily disturbed sites where it may form monospecific stands (Fig. 4-70).

Myrmecophily of *N. gigantea* has first been reported by WINKLER (1910) but taxonomic identity of the ants colonising the caulinary domatia remained unknown. Here, two *Cladomyrma* species are identified inhabiting *N. gigantea*, predominantly *C. dianeae* and *C. aurochaetae* (one collection). Most likely, records of other *Cladomyrma* species will be added both by future sampling and by elaborating a species key based on the worker caste of *Cladomyrma*. A few *Crematogaster* species are capable of colonising abandoned trees or displacing the resident *Cladomyrma* colony, and, in some localities, turnover of ants caused by disturbance of established colonies (predation on ants) appears to be high (see above). An unquantified proportion of *N. gigantea* trees reaches maturity (reproductive stage) without ant inhabitants: (i) mature trees were found growing outside the altitudinal limit of *Cladomyrma* in elevations between 1,300-1,650 m, or (ii) isolated populations that either never had or had lost their ant partner were too distant from rainforest sources for (re-)colonisation.

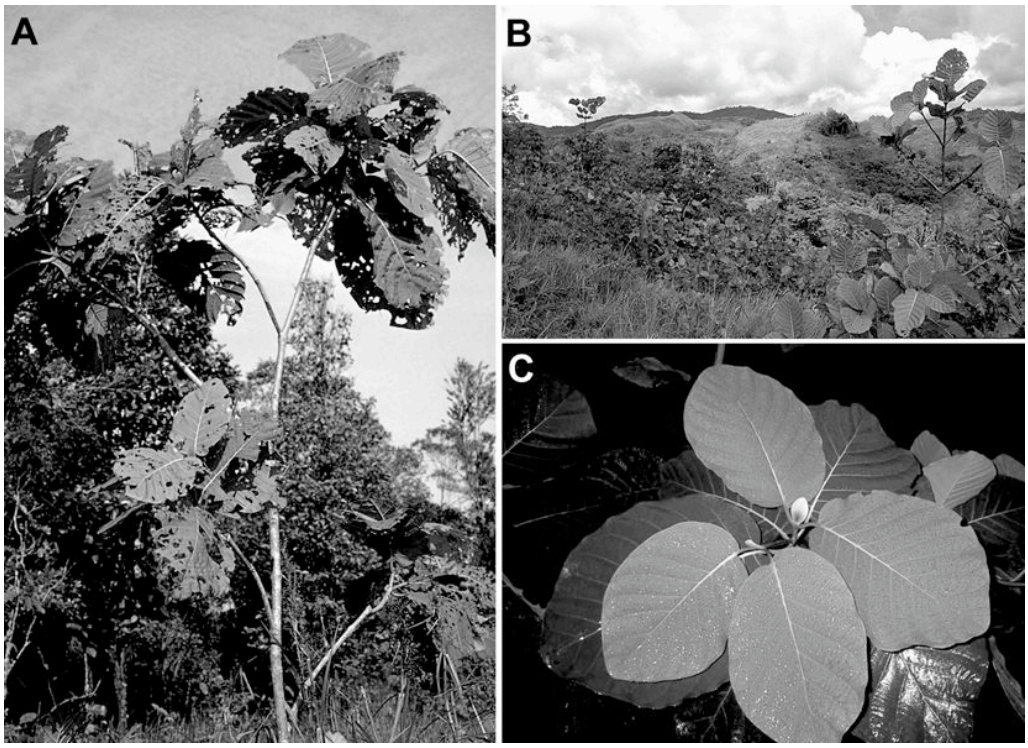


Figure 4-70: Habitat and habit of Bornean *Neonauclea gigantea*. **A**: Roadside tree 4 m tall (N-019), with 8 domatia in total of which only one contained a dead *Cladomyrma* foundress; the remaining 7 domatia were uninhabited and solid. Following a road leading away from an old secondary forest into agricultural land it was the last tree on which *Cladomyrma* was present (5 km distance to forest). Note the heavy level of folivory. **B**: monospecific stand of *N. gigantea* in a habitat characterised by fragments of logged over forest, plantations and fallow land at about 900 m altitude. Here, occupancy rate of trees by *Cladomyrma* was variable (high disturbance regime). **C**: shoot of a riverside tree, about 12 m in height, colonised by a healthy, mature *Cladomyrma* colony within an old secondary forest.

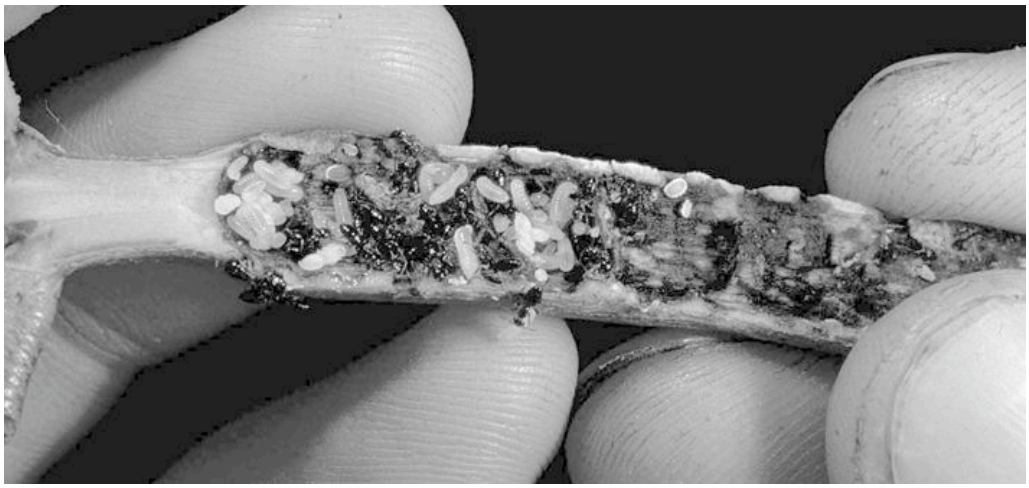


Figure 4-71: Dissected domatium of *Neonauclea gigantea*, showing workers and brood of *Cladomyrma dianeae* as well as some mealybugs.

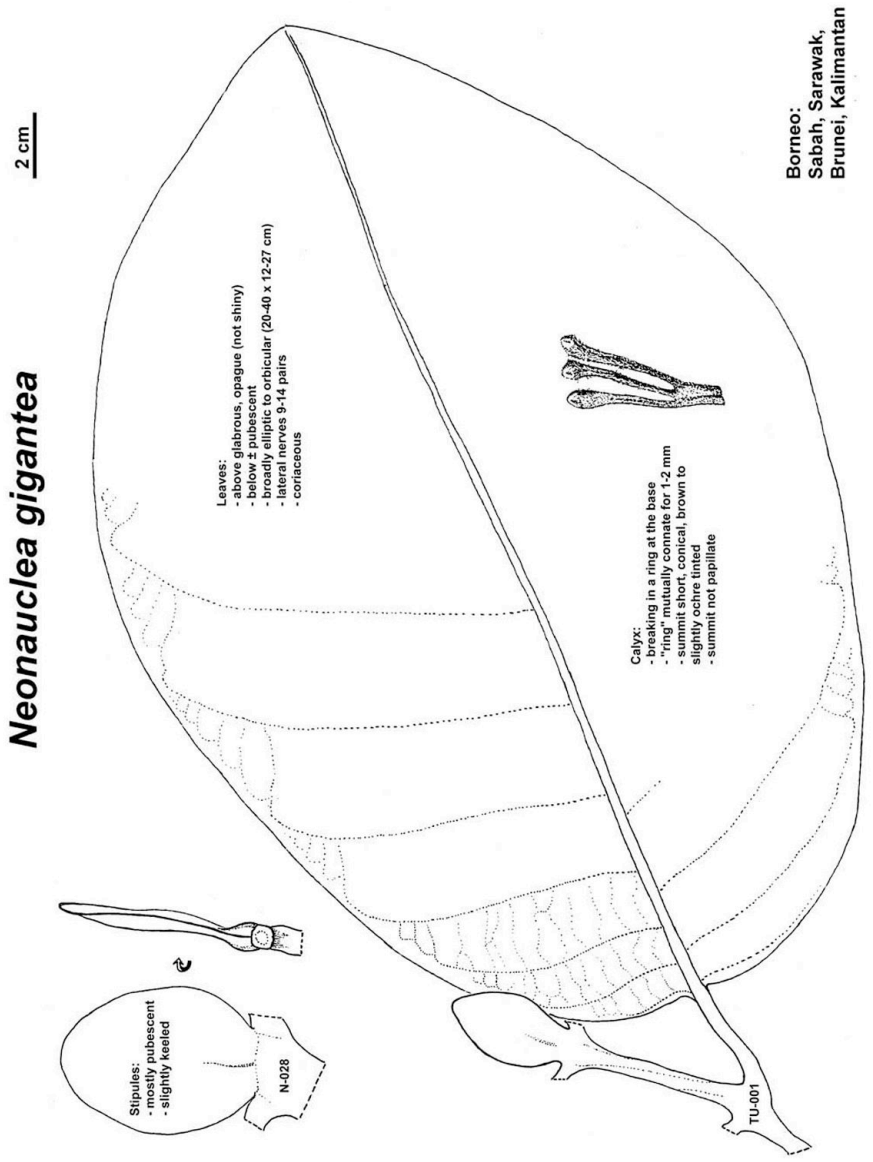


Figure 4-72: *Neonauclea gigantea*; stipules, leaf and calyces. Drawing: J. Moog.

Neonauclea longipedunculata Merrill

Figure 4-73

Tree up to 30 m; common. Habitat: primary and secondary forest, riverside, logging paths, and roadside; lowlands to 400 m altitude. Distribution: Borneo (Sabah, Brunei [two collections], Kalimantan [close to Sabah border; one collection]). Note: Trees of *N. longipedunculata* were often found growing in association with *N. gigantea* along the Ranau - Telupid road (Sabah). Although adapted to pioneer habitats, the species seems to prefer somewhat less heavily disturbed sites than *N. gigantea*. Establishment of *N. longipedunculata* seedlings in recently logged sites has been studied by PINARD, HOWLETT & DAVIDSON (1996) at the Ulu Segama Forest Reserve (Sabah).

I have identified two *Cladomyrma* species, *C. dianeae* and *C. hewitti*, as regular inhabitants of *N. longipedunculata*. A single tree, characterised by a conspicuous high level of folivory, was found to be inhabited by a huge *Crematogaster* colony. The tree grew among a group of similar-sized *Neonauclea* trees (*N. longipedunculata* and *N. gigantea*), all of which were colonised by *Cladomyrma* ants. Examination of several domatia housing *Crematogaster* ants suggest that they were formerly occupied by *Cladomyrma*.

Neonauclea paracyrtopoda Bakh. f. & Ridsdale

Figure 4-74

Small tree, rarely attaining 15 m. Habitat: primary and secondary forest, riverside, hillside, and forest edge; lowlands to 500 m altitude. Distribution: Borneo (Sarawak, Brunei, Sabah [close to Brunei border; one collection]). Note: The species is common at Lambir Hills NP, Sarawak, often at forest edges. At this location, *Cladomyrma dianeae* ants were found to inhabit the domatia of *Neonauclea paracyrtopoda*. In addition, I collected other ant taxa such as *Crematogaster* and *Camponotus* (*Colobopsis*) from abandoned *Cladomyrma* chambers. Some trees at Lambir had domatia heavily damaged, possibly by a predator of ants and/or their brood.

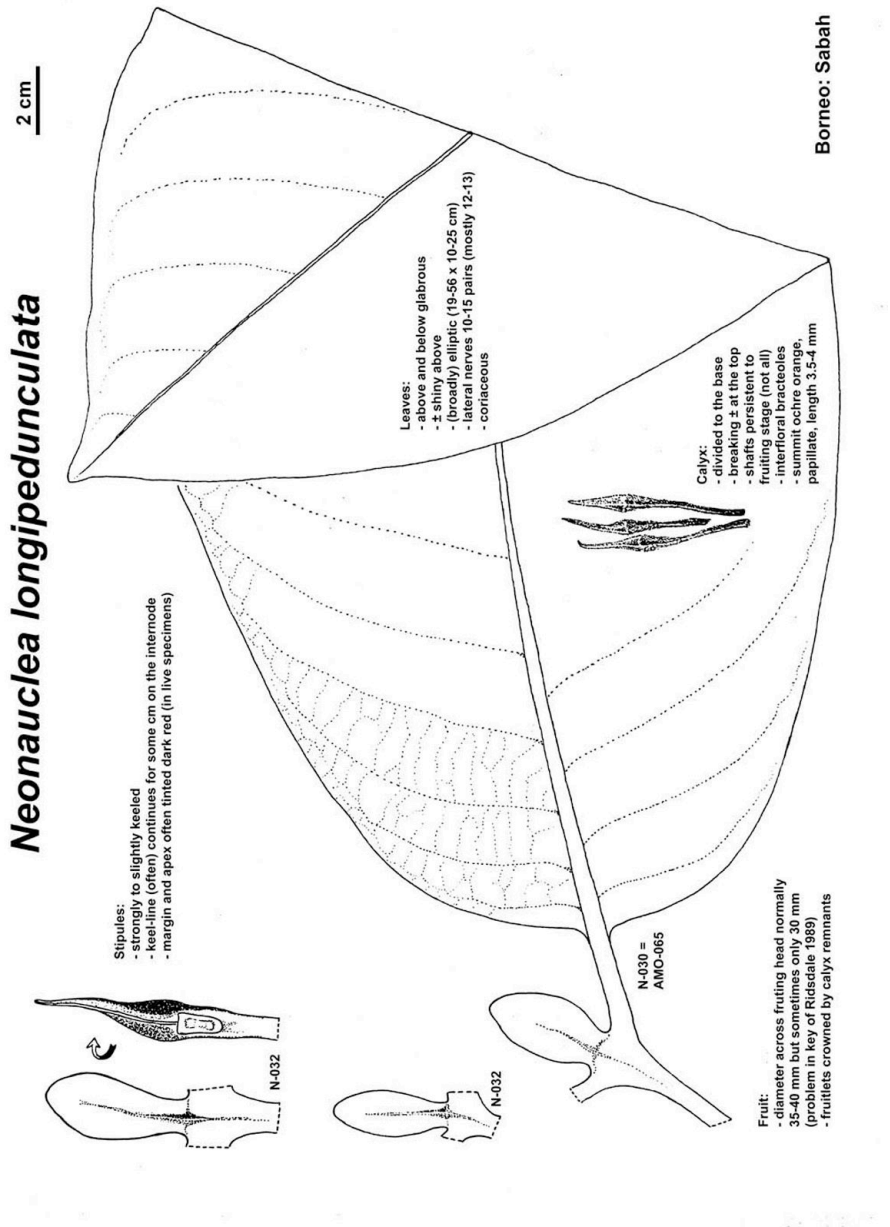


Figure 4-73: *Neonauclea longipedunculata*; stipules, leaf and calyces. Drawing: J. Moog.

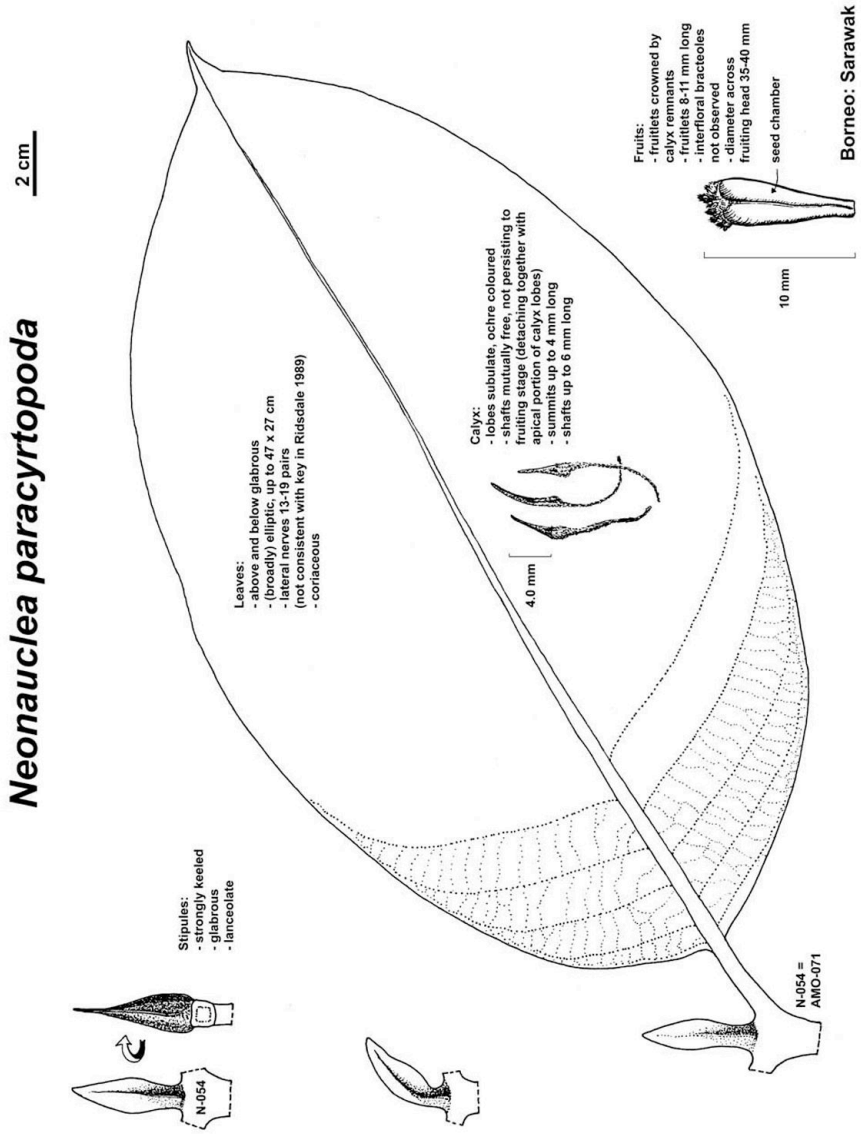


Figure 4-74: *Neonauclea paracyrtopoda*; stipules, leaf, calyces and fruitlet. Drawing: J. Moog.

Neonauclea pseudocalycina Ridsdale

Figure 4-75

Tree up to 25 m; locally common. Habitat: ridges in primary and secondary forest, riverine forest, hillside, slopes, roadside, and 'Agathis forest' (one coll.); about 200 to 1,500 m altitude. Distribution: Borneo (Sabah, Sarawak, Kalimantan), Philippines (Tawi Tawi island, close to Sabah border). Note: *Neonauclea pseudocalycina* has been recorded from the Mount Kinabalu area (Sabah) at altitudes between 1,000 to 1,400 m. My own observations in the same area suggest that a population of a *Neonauclea* species, closely resembling *N. pseudocalycina* in vegetative characters, attains elevations of 1,500 m and still produces domatia in the absence of their *Cladomyrma* ant partner which does not exceed altitudes of ca. 1,300 to 1,400 m. Below their elevational limit I collected *Cladomyrma* ants inhabiting *N. pseudocalycina* in the Crocker Ranges (Sabah) which I identified as members of the species *C. hewitti*.

***Neonauclea* sp. A**

Figure 4-76

Small tree. Habitat: riverside in primary and secondary forests, roadside, and degraded areas such as log landings; ca. 400–800 m altitude. Distribution: Borneo (Sabah). Note: This informal species could not be matched with one of the myrmecophytic *Neonauclea* species known from Borneo because only sterile material was available. The specimens collected in the field had comparatively small leaves with a shiny adaxial surface and rather small, lanceolate stipules (Fig. 4-76). *Neonauclea* sp. A, predominantly found in the Ranau area (Sabah), was regularly occupied by unidentified *Cladomyrma* ants. Ocassionally, a polydomous *Crematogaster* species was found that had built carton nests on the leaf underside of non-occupied trees. In these cases, it is supposed that the expansion of the *Crematogaster* nest from neighbouring plants onto trees of *Neonauclea* sp. A prevented the successful colonisation of sp. A by *Cladomyrma* foundresses.

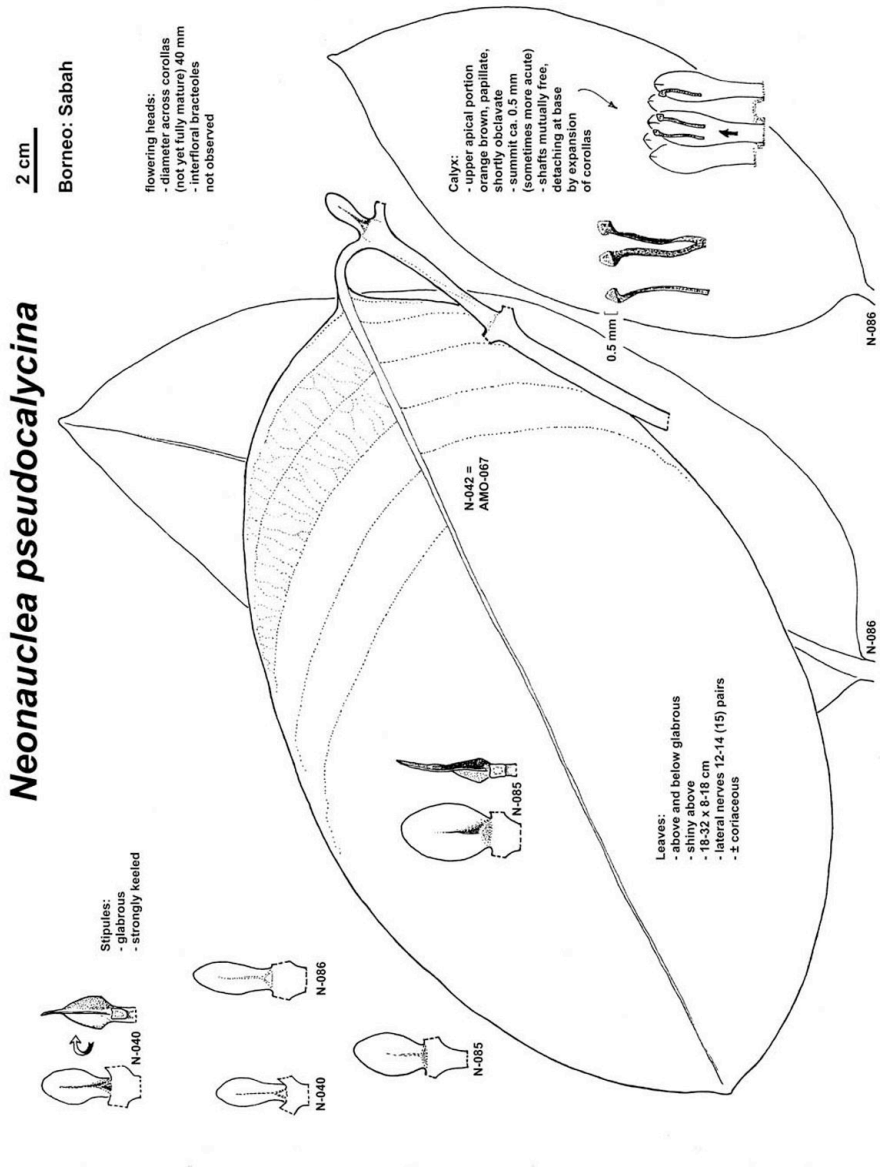


Figure 4-75: *Neonauclea pseudocalycina*; stipules, leaves and calyces. Drawing: J. Moog.

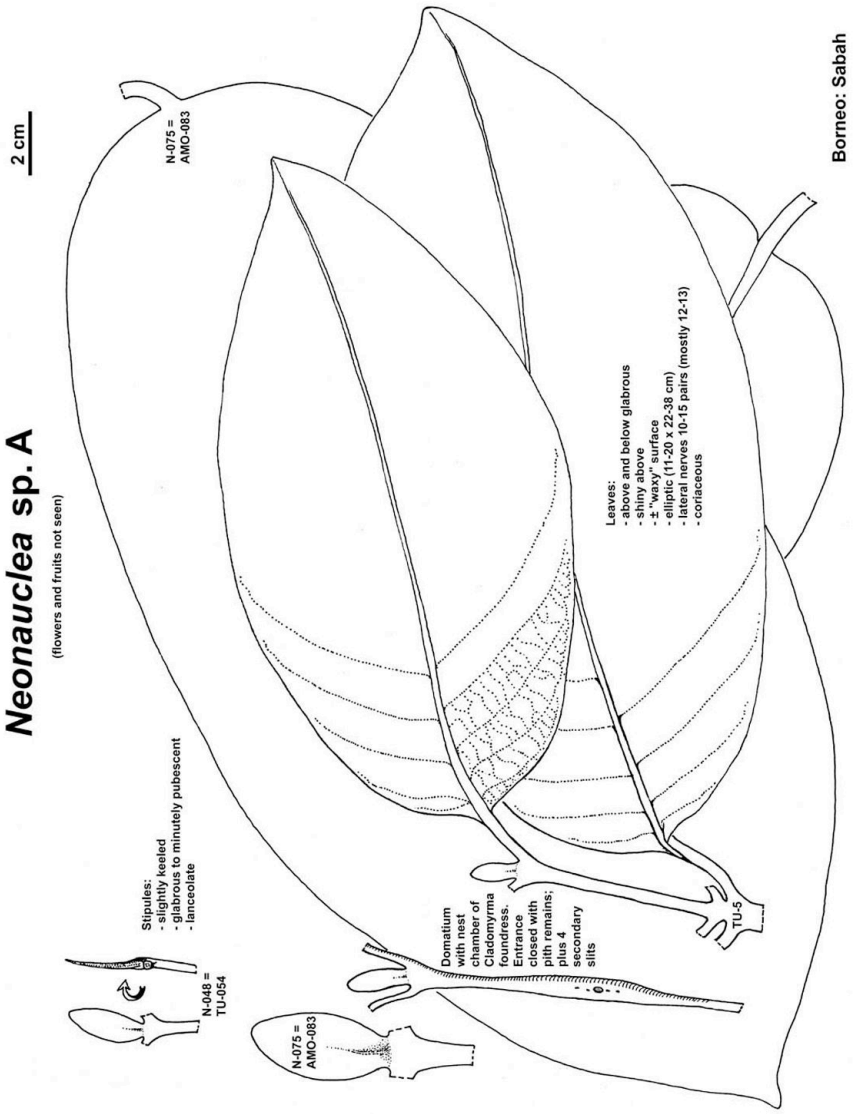


Figure 4-76: *Neonauclea* sp. A; stipules, leaves and domatium. Drawing: J. Moog.

***Neonauclea* sp. B**

Figure 4-77

Tree up to 12 m. Habitat: disturbed forests, roadside, gaps; only known from altitudes of ca. 900 to 1,400 m. Distribution: Borneo (Sabah). Note: *Neonauclea* sp. B appears to be adapted to fairly high elevations. It has ± coriaceous leaves (7–17 x 15–31 cm) with usually 10 to 14 pairs of lateral nerves. The species, often scattered among *N. gigantea* trees, is common along the Kota Kinabalu - Ranau road below the junction to the Kinabalu Headquarter. Possibly due to factors such as the high altitude and the distance to forests only a rather small proportion (c. 30%) of the specimens found at this locality were inhabited by (unidentified) *Cladomyrma* ants.

Figure 4-77: Dried specimen of *Neonauclea* sp. B, tree 12 m in height; AMO-037, km 36 east of Ranau, Sabah, Borneo; leg. Joachim Moog/Tina Urschek. Domatia inhabited by *Cladomyrma* ants. Scale bar: 5 cm.

***Neonauclea* sp. C**

Figure 4-78

Small tree. Habitat: primary and secondary forests, often along creeks, small gaps; only found between 500 to 800 m altitude. Distribution: Borneo (Sabah). Note: Sterile specimens of *Neonauclea* sp. C are easy to recognise with their distinctively spathulate stipules and ± chartaceous, obovate leaves. This species has been found primarily in rather shady habitats of the understorey at Poring Hot Springs (near Ranau). *Cladomyrma maryatiae* appears to be the dominant ant partner but *C. dianeae* has also been recorded once. Current collections also include *Crematogaster* and *Technomyrmex* ants from domatia previously occupied by *Cladomyrma* foundresses.

***Neonauclea* sp. D**

Figure 4-79

Small tree. Habitat: understorey of primary and secondary forest, small gaps; known from elevations of 500 to 900 m. Distribution: Borneo (Sabah). Note: Sterile young plants of *Neonauclea* sp. D closely resemble those of sympatric *Neonauclea* sp. C in overall appearance. Several features seem to separate the two 'species', however. Stipules tend to be circular rather than spathulate, leaves are (broadly) elliptic with rounded to cuneate bases rather than obovate (Fig. 4-79) and their number of lateral nerves is usually smaller. However, the extent of variation in these characters may be greater than currently judged from a low field sample. The species is associated with *Cladomyrma maryatiae* and an unidentified member of the genus.

***Neonauclea* sp. E**

Figure 4-80

Small tree. Habitat: limestone, secondary vegetation, roadside; lowlands. Distribution: Borneo (Sabah, N Sarawak). Note: This species closely resembles *N. excelsioides* in the stipules and several leaf characters (e.g., size, texture, number of lateral nerves), and may be identical with *N. excelsioides*. Sp. E was primarily found on limestone at the Niah Caves (N Sarawak) but has also been collected in Sabah east of Telupid. Ant inhabitants collected belonged to *Cladomyrma* sp., *C. dianeae* and a generalist carton-building *Crematogaster* species (one coll.).

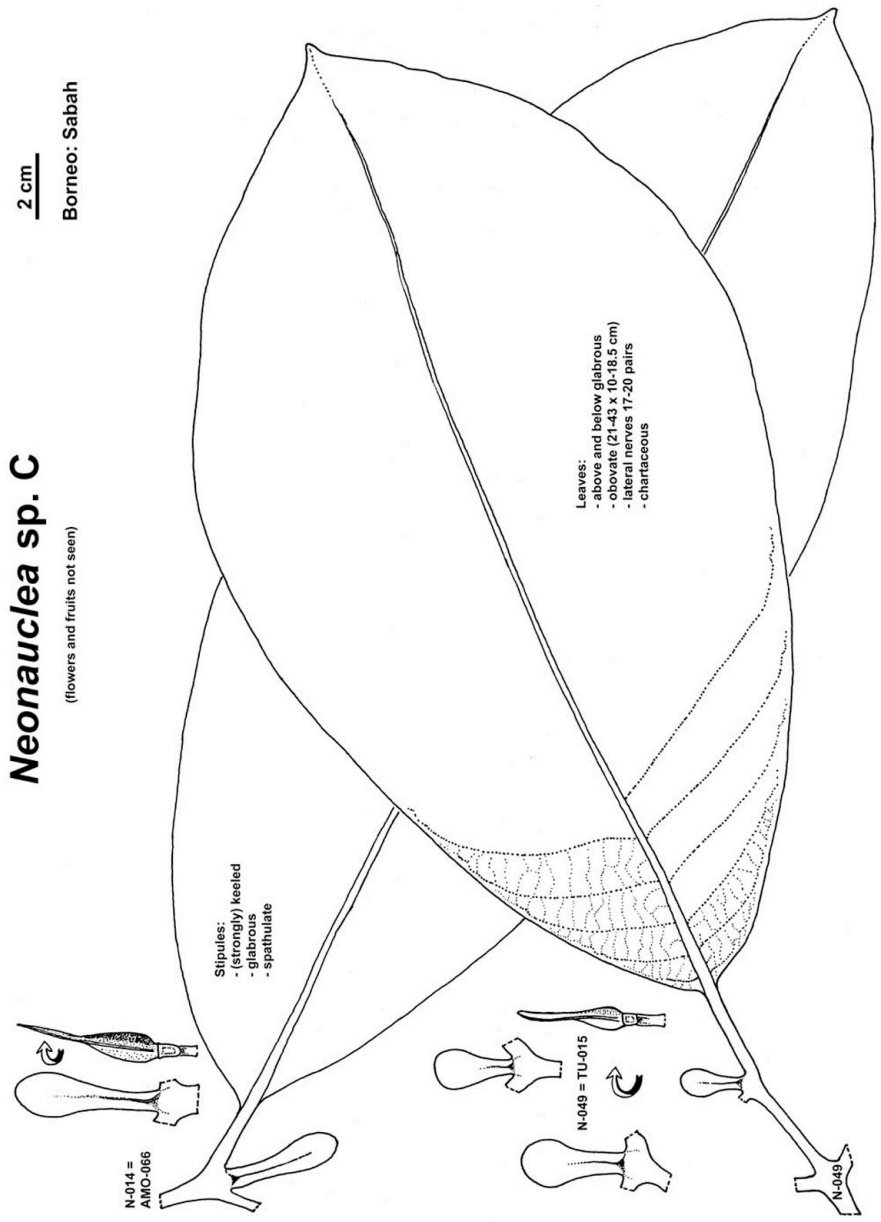


Figure 4-78: *Neonauclea* sp. C; stipules and leaves. Drawing: J. Moog.

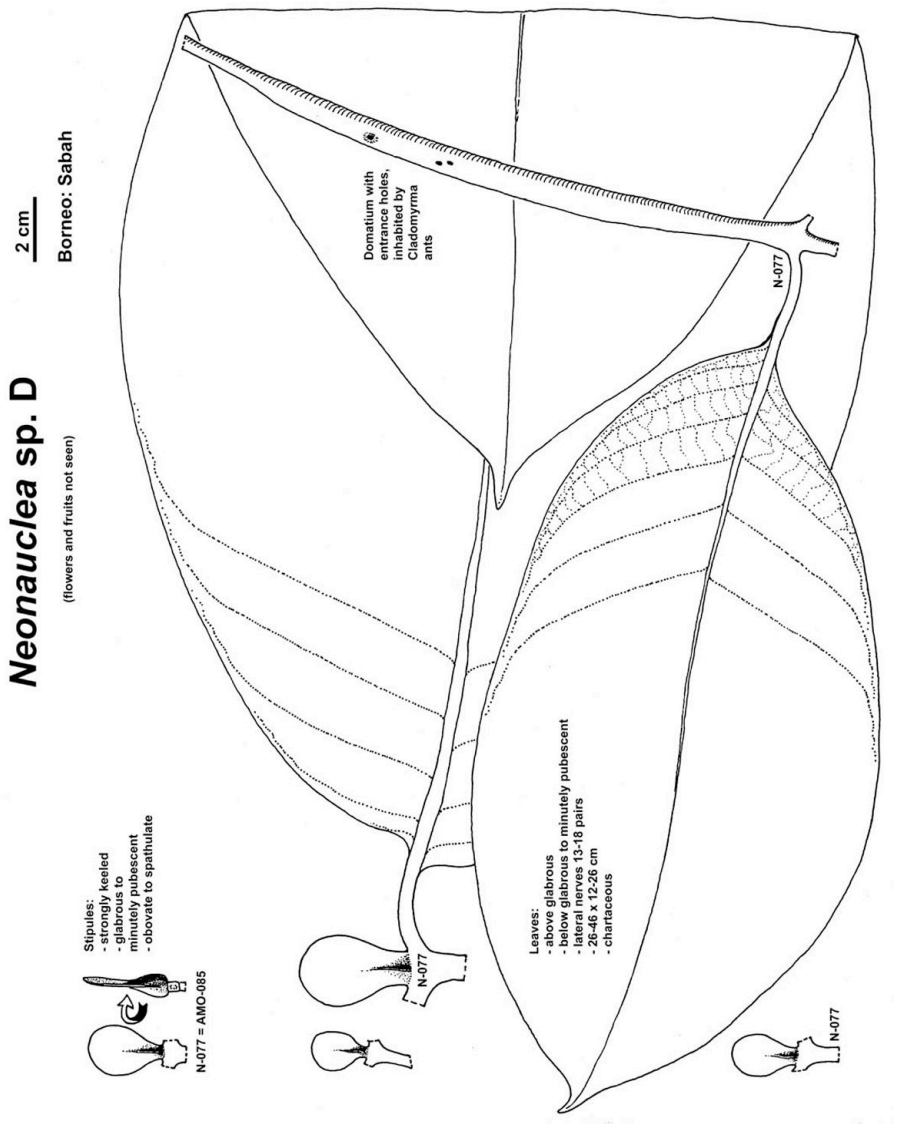


Figure 4-79: *Neonauclea* sp. D; stipules, leaves and domatium. Drawing: J. Moog.

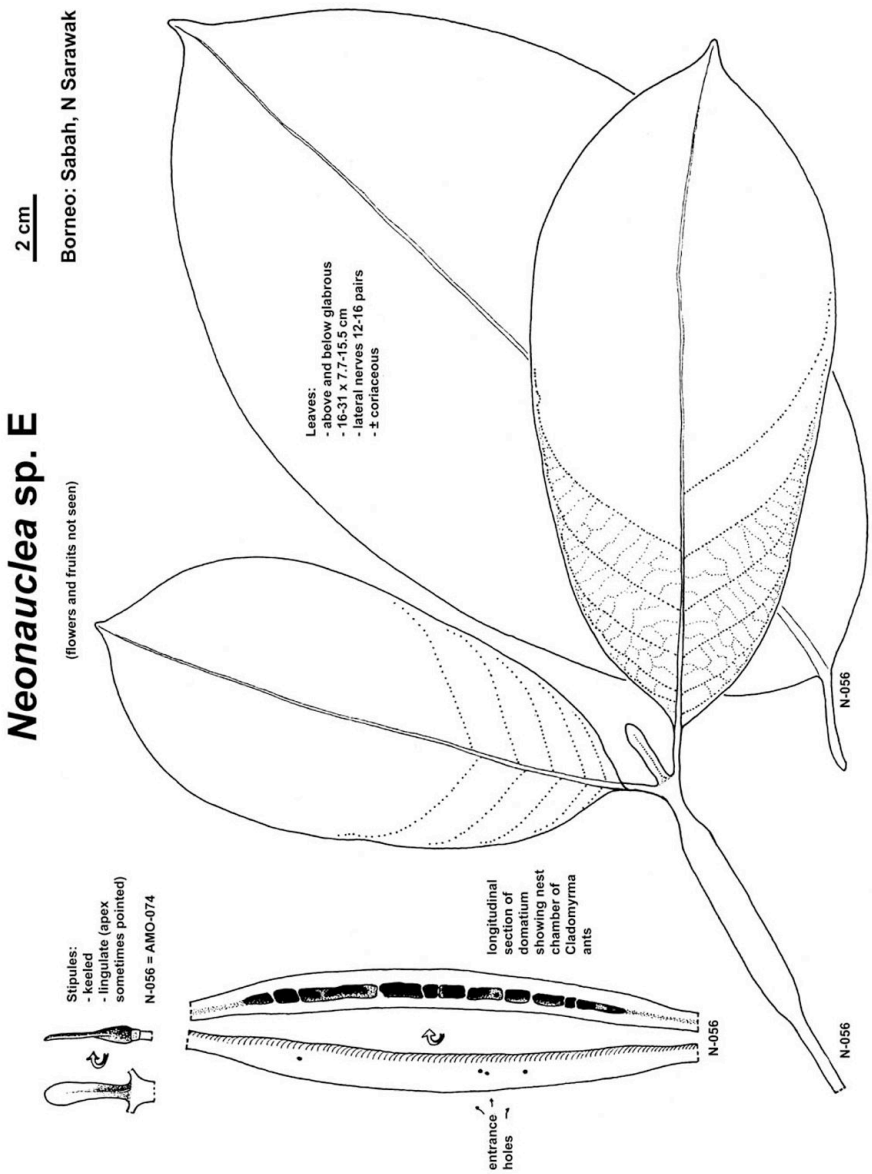


Figure 4-80: *Neonauclea* sp. E; stipules, leaves and domatium. Drawing: J. Moog.

4.3.9. Summary of the results: host plants

- 24 plant species belonging to 10 genera and 8 families are recognised as hosts of *Cladomyrma* ants
- for each genus the number of species regularly occupied by *Cladomyrma* is 8 (*Neonauclea*), 4 (*Ryparosa*), 2 (*Crypteronia*, *Drypetes*, *Saraca*, *Spatholobus*), and 1 (*Callerya*, *Luvunga*, *Strychnos*). Not known for *Sphenodesme*
- *Cladomyrma* hosts include woody climbers and trees; overall, they show a great ecological amplitude ranging from pioneer habitats to the rainforest understorey
- structures to house ants are distinctly different among host taxa and cover the whole range from apparently unmodified twigs to strongly swollen stem domatia containing a soft pith that is easily excavated by the ants
- in some taxa the domatia are only distinct in young sterile saplings and, therefore, are absent from flowering herbarium material
- prostomata, i.e., 'weak spots' through which ants gain access into the stem, are only developed in species of the host genus *Neonauclea*
- in all hosts, *Cladomyrma* tends trophobiotic scale insects inside the stems (never on the plant's surface); direct food sources for the ants –such as food bodies or extrafloral nectar– are not provided by the hosts (but see *Ryparosa* and *Saraca*)
- generally, *Cladomyrma* is always the first coloniser of its hosts, and onset of occupation occurs early in the ontogeny of the host plants (depending on primary twig diameter in relation to foundress size)
- the occupancy rate of a host species is usually high but may vary according to factors such as plant age, colony life expectancy, interspecific competition with alien ants, and myrmecophagy by predators
- the host *Strychnos vanprukii* has a comparatively low occupancy rate and may represent a present host expansion process by *Cladomyrma petalae*
- some host species occasionally occur outside the range of their *Cladomyrma* ant partners, i.e., when hosts are growing isolated and distant from rainforest sources or when the plant's elevational limit exceeds those of the ants

4.4. DISCUSSION

During the scientific exploration of the south-east Asian tropics in the 19th Century, botanists returned from their expeditions with collections of most curious plants with hollow structures (myrmecodomatia) seemingly designed to favour ant occupation (JACK 1823, BECCARI 1877-1883, 1884-1886, 1885, BOWER 1887, SCHUMANN 1889 and 1890, WARBURG 1892 and 1894). Within the first half of the 20th Century reports of many new plant species regularly found associated with ants accumulated (SCHUMANN & LAUTERBACH 1901, YAPP 1902, SMITH 1903, RIDLEY 1910, KERR 1912, DOCTERS VAN LEEUWEN 1929a+b, MERRILL 1929, MERRILL & PERRY 1940), but with time the interest in these unusual plants diminished. Thus the number of known ant-plants in south-east Asia remained on a low level.

In the 70's and 80's the existing knowledge of ant-plants in the region was revisited (JOLIVET 1973, 1986) and some of these associations –such as the ant-epiphytes– were studied in detail for the first time (JANZEN 1974, HUXLEY 1978). But it was not until the pioneering work of U. MASCHWITZ, B. FIALA and co-workers in the 90's that our knowledge on the number and natural history of non-epiphytic myrmecophytes in south-east Asia increased considerably (e.g., MASCHWITZ et al. 1989, 1994, 1996a-b, ZIZKA, MASCHWITZ & FIALA 1990, MASCHWITZ, FIALA & LINSENMAIR 1992, 1994, MASCHWITZ & FIALA 1995, FIALA et al. 1989, 1999, FIALA, MASCHWITZ & LINSENMAIR 1996, JANKA et al. 2000). Likewise, the ant-epiphytes of the region became increasingly known through studies by e.g., RINTZ 1978, 1980, DAVIDSON & EPSTEIN 1989, HUXLEY & JEBB 1991a-c, GAY et al. 1993, KIEW & ANTHONYSAMY 1995, WEISSFLOG et al. 1999, KLEIJN & DONKELAAR 2001, and KAUFMANN 2002, 2006.

This study summarises the new findings on *Cladomyrma* hosts that accumulated over the last two decades. Since *Cladomyrma* has a cryptic lifestyle within stem cavities, the methodical search for ant entrances in plant stems both in the field and in herbarium specimens revealed a large number of host plant taxa. Presently, the hosts of *Cladomyrma* make up about 50% of all non-epiphytic plant genera which are known to be regularly associated with specialised stem-nesting ant partners in the Oriental region (MOOG et al. 2003).

From table 4-6 it is apparent that diversity of hosts can be viewed in terms of descent (taxon), distribution, habitat, growth form or ant-housing structures.

Table 4-6: List of host plants colonised by *Cladomyrma* ants. Host plant taxa: Superscript = altitudinal range of plants found associated with *Cladomyrma* (meter a.s.l.): **1** = 0–500, **2** = 500–900, **3** = 900–1300; growth form: **L** = liana, **T** = tree, **c** = canopy, **u** = understorey; habitat: **e** = edge, second growth, **g** = forest light gaps, **p** = primary forests, **l** = limestone, **r** = riparian environments, **s** = advanced secondary growth; structures to house ants: **D** = domatia (strongly swollen internodes), **hS** = naturally hollow stems (in part), **pS** = pithy stems, hollowed by ants, **sN** = slightly thickened nodes, **tN** = thickened nodes, **sI** = swollen internodes in saplings; region: **B** = Borneo, **MP** = Malay Peninsula, **SU** = Sumatra, **TH** = Thailand, **V** = Vietnam. Asteriks ***** = based on herbarium specimens only. ** In total, eight *Neonauclea* species are described from Borneo, of which five –all hosts of *Cladomyrma*– could be identified to species level. The three remaining species (*N. artocarpoides*, *N. calcarea*, *N. excelsioides*) may be represented by the species informally named A, B, C, D, and E in this work. Undet. = undetermined species (remains of *Cladomyrma* workers have been found in herbarium material of *Ryparosa porcata*; specimens of *Ryparosa anterides*, *R.* sp. nov. aff. *calotricha*, *Crypteronia macrophylla* and *Drypetes fusiformis* possess entrance holes typical of *Cladomyrma* occupation).

host plant species	growth form	habitat	structures to house ants	*Cladomyrma* species	geographic region
ACHARIACEAE					
**Ryparosa anterides* [1]	T	l, s, p, r	pS, tN	undet.	B
R. fasciculata [1-2]	T, u	s, p	pS, sN	*nudidorsalis*, *petalae*	MP
**R. porcata* [1]	T, u	s, p	pS, sN	undet.	B
**R.* sp. nov. aff. *calotricha* [1]	T, u	s, p	pS	undet.	B
CRYPTERONIACEAE					
Crypteronia griffithii [1-2]	T, u, (c)	g, s, p	pS, tN	*crypteroniae*, *maschwitzi*	B, MP, SU
**C. macrophylla* [1-3]	T, u	?p	pS, tN	?*crypteroniae*, ?*maschwitzi*	B
FABACEAE					
Callerya nieuwenhuisii [1-3]	L, u, c	g, s, p, r	pS, sI	*andrei*	B
Saraca dives [1-2]	T, u	s, p, r	pS, sN	*scopulosa*	V
S. thaipingensis [1-2]	T, u	s, p, r	pS, tN	*petalae*	MP
Spatholobus bracteolatus [2-3]	L, u, c	s, p	pS, sI	*petalae*	MP
S. oblongifolius [1-3]	L, u, c	s, p	pS, sI, tN	*andrei*, *hobbyi*, ?*maryatiae*	B
LOGANIACEAE					
Strychnos vanprukii [1]	L, u	s, p	pS, hS	*petalae*	MP
PUTRANJIVACEAE					
Drypetes longifolia [1-3]	T, u	s, p	pS, sI, D	B: *andrei*, *hobbyi*, *yongi* MP: *petalae*, *nudidorsalis*	B, MP
**Drypetes fusiformis* [1]	T, u, (c)	s, p, ?r	pS, ?sI	undet.	B
RUBIACEAE					
Neonauclea borneensis [1-2]	T, u	e, s	pS, D	*dianeae*	B
N. gigantea [1-3]	T, (c)	e, g, r	pS, D	*aurochaetae*, *dianeae*	B
N. longipedunculata [1-2]	T, (c)	e, g, r	pS, D	*dianeae*, *hewitti*	B
N. paracyrtopoda [2]	T, u	e, g, r	pS, D	?*dianeae*	B
N. pseudocalycina [2]	T	e, g, r	pS, D	*hewitti*	B
** 3(+) *Neonauclea* spp. [1-2]	T, u, (c)	e, g, l, p, r	pS, D	*dianeae*, *maryatiae*	B
RUTACEAE					
Luvunga sp. [1-2]	L, u, (c)	s, p	pS, sI	*petalae*	MP
LAMIACEAE					
Sphenodesme sp. [1-2 ?]	L	?	?	undet.	TH

4.4.1. Taxonomic diversity

The hosts of *Cladomyrma* consist of a broad range of mostly unrelated species, indicating multiple, separate origins of myrmecophytism. Overall, 24 plant species belonging to 10 genera and eight families are recognised here as hosts of *Cladomyrma* (Tab. 4-6). The broad host range suggests that more hosts await discovery by sampling in remote localities or in countries of Continental Asia (see recent collections from Thailand and Vietnam). Although this study raises the possibility that hosts might be still more diverse than is currently known, both observations in the field and the examination of nearly 5,000 herbarium specimens of congeneric host taxa showed that *Cladomyrma* is certainly not a "jack-of-all-trades", i..e, the ant does not colonise every available plant with a suitable primary twig diameter (see also paragraph 11.5. on host specificity, p. 317). The great majority of host taxa is regularly occupied by *Cladomyrma* only, other ant taxa sometimes play a minor role as secondary colonisers. Ant-plant species in the genus *Neonauclea* (Rubiaceae) are an exception as some are known to harbour specialist *Crematogaster* ants outside the range of *Cladomyrma*. It is also the only host genus with a significant radiation of ant-plants (17, of which eight are associated with *Cladomyrma*). In terms of taxonomic diversity on the genus and family level the range of hosts utilised by *Cladomyrma* is one of the broadest ever recorded for any live stem-nesting plant-ant lineage worldwide.

4.4.2. Diversity in distribution

If we examine the distribution of individual hosts of *Cladomyrma* several patterns become apparent. First, all, except one (see below), of the 24 plant species do not cross Wallace's line. Second, center of host diversity is Borneo with 17 species, followed by the Malay Peninsula with seven species. Third, the recently found host plants *Sphenodesme* sp. (East Thailand) and *Saraca dives* (North Vietnam) indicate that the association between *Cladomyrma* and plants, previously only known from the aseasonal wet forests, also occur in the seasonal climatic zones of Continental Asia. Fourth, most species are endemic to Borneo or the Malay Peninsula, only four are found over a larger geographical scale (in part because species boundaries of taxa are unclear):

1.) *Crypteronia griffithii*, distributed in Sumatra, the Malay Peninsula and Borneo, has stem-dwelling *Cladomyrma* associates in all three geographic areas; 2.) *Saraca thaipingensis*, a species found in association with *Cladomyrma* throughout the Malay Peninsula reaches north of the Isthmus of Kra (southern Myanmar) and west to Java. Yet herbarium material of *S. thaipingensis* from both the Isthmus of Kra (n=2) and Java (n=9) showed no signs of ant inhabitation; 3.) *Strychnos vanprukii* is a wide-

ranging species that occurs in south and northeast India, Laos, Vietnam, Thailand, Malay Peninsula and Borneo. Herbarium specimens collected outside the Malay Peninsula (n=10) showed no indication for ant occupancy. The Malayan material differs in vegetative characters from the remaining specimens collected in Continental Asia and Borneo and the taxonomic problems (see page 76) should be redressed; 4.) The tree *Drypetes longifolia*, the only host crossing Wallace's line, has been circumscribed as a widespread species, found from India, Sri Lanka, Andamans, Myanmar, and throughout Malesia to New Guinea. To my knowledge, however, ant association of *D. longifolia* from areas outside the Malay Peninsula and Borneo has never been reported (e.g., India: CHAKRABARTY, GANGOPADHYAY & BALAKRISHNAN 1997; Sumatra: AIRY SHAW 1982; Java: BACKER & BAKHUIZEN VAN DER BRINK 1963; Philippines and Sulawesi: PAX & HOFFMANN 1931; Moluccas: EDWARDS et al. 1990; New Guinea: AIRY SHAW 1980). A thorough inspection of herbarium specimens of this species collected east of Wallace's line and west of the Malay Peninsula support the lack of a regular ant-association. Of 73 specimens examined only three possessed hollow stem sections and holes. They were collected in Papua New Guinea (SAUNDERS 393, 519 and NGF 10313A). Although I cannot exclude that New Guinean *D. longifolia* may occasionally be occupied by ants (3 of 19 specimens had signs of ant inhabitation), the stem holes did not resemble those made by *Cladomyrma* ants. As I pointed out earlier (page 103) the currently recognised circumscription of *Drypetes longifolia* is problematic and may include a number of recognisable segregate taxa that warrant specific recognition.

4.4.3. Diverse habitats

Habitats from which host plants have been recorded are highly variable, both along an horizontal and an elevational gradient (Tab. 4-6, Fig. 4-81). They are often found in areas of natural disturbance which are embedded in primary and advanced secondary forest such as river margins (*Saraca*), landslides and tree fall gaps (*Crypteronia*). One host plant, *Neonauclea calcarea*, appears to be specialised to limestone habitat. Occasionally, *Ryparosa porcata* and *Drypetes fusiformis* have been recorded from forest over limestone. Some host species grow in the shaded forest understorey (*Ryparosa*, *Strychnos*), others can invade large man-made disturbances, sometimes dominating in early successsional vegetation and forest patches surrounded by agricultural land (*Neonauclea gigantea*). This high ecological amplitude of *Cladomyrma* host plant species can also be seen at an intraspecific level. For instance, hosts such as *Callerya nieuwenhuisii*, *Spatholobus oblongifolius*, and some *Neonauclea* spp. are regularly found along creeks and rivers, although a considerable part of the collections are recorded from well-drained steep slopes and hill ridges covered by forest. Also, light-demanding *Neonauclea* host species, that form a typical

element of Bornean wayside vegetation, are commonly found as relatively shade-tolerant juveniles in the understorey.

Host plants have been found from sea level to the elevational limit of *Cladomyrma* at ca. 1,350 m. In two species, *Neonauclea pseudocalycina* and *Neonauclea gigantea*, plants occured at altitudes of up to 1,500 and 1,650 m, respectively, well above the limit of the associated ant (Fig. 4-81). All plants had produced domatia whose interior was solid and uninhabited.

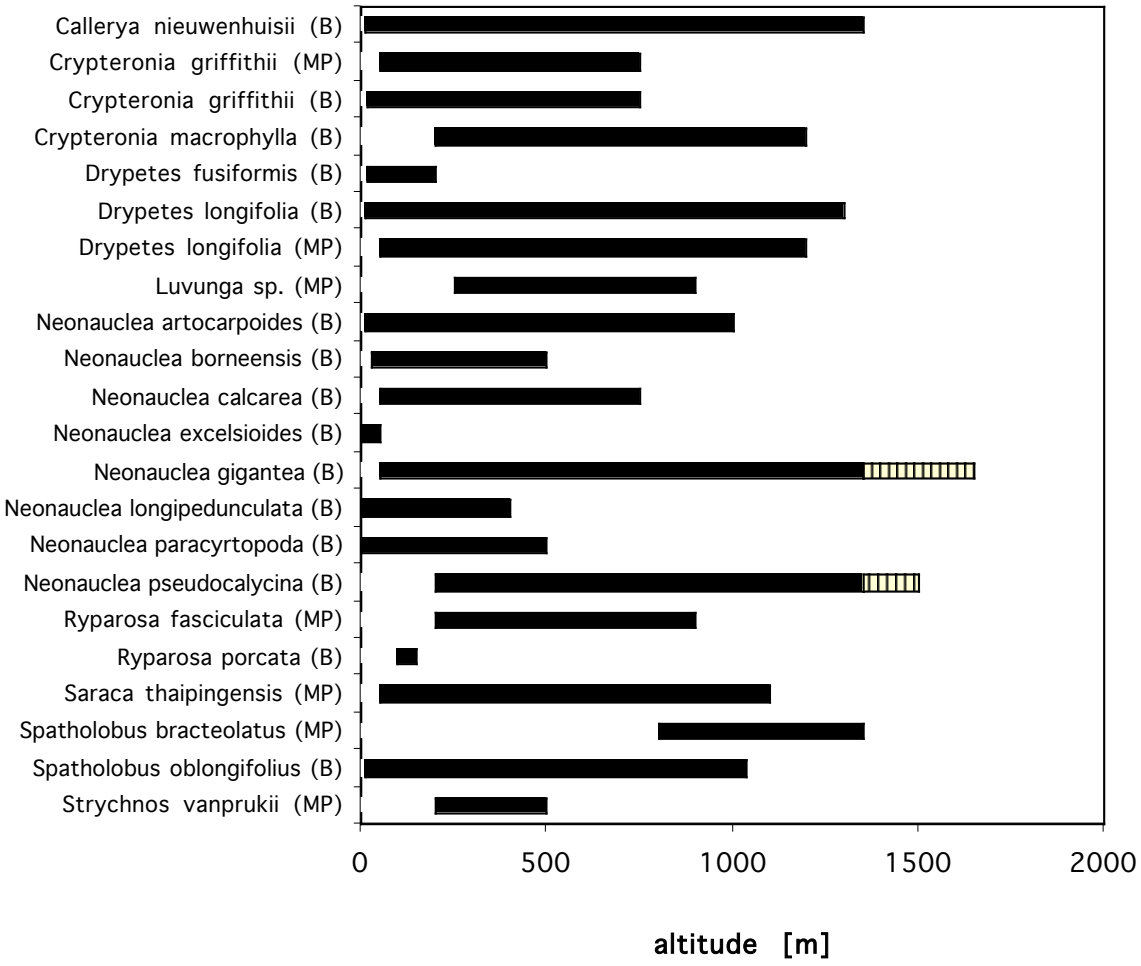


Figure 4-81: Altitudinal range of *Cladomyrma* host plants as derived from field and herbarium data (dark bars). Ranges of plant species above the elevational limit of *Cladomyrma* (ca. 1,350 m) are given as light bars. MP = Malay Peninsula, B = Borneo. [The narow altitudinal range of host plants such as *Neonauclea excelsioides* and *Ryparos porcata* is likely an effect of low sample size.]

Most host plants are adapted to low and mid-elevations. Interestingly, the upper elevational limit of *Callerya nieuwenhuisii* and *Spatholobus bracteolatus* appears to

coincide with that of the associated *Cladomyrma* species. The latter host, a woody climber, is also remarkable in that it is not found below 800 m. Its inhabitant is *Cladomyrma petalae*, the regular partner ant of *Saraca thaipingensis* at lower altitudes. In the elevationally zone of sympatry both hosts are colonised. At one site (Fraser's Hill, Selangor, Malay Peninsula), in a small elevational band at 800 m, I collected *Cladomyrma petalae* from five sympatric hosts (*Drypetes longifolia*, *Luvunga* sp., *Ryparosa fasciculata*, *Saraca thaipingensis*, *Spatholobus bracteolatus*). The narrow altitudinal range exhibited by hosts such as *Ryparosa porcata* or *Neonauclea excelsioides* is probably due to the small sample available.

A similar altitudinal zonation of obligate myrmecophytes and associated ants with an upper limit at about 1,250 m has been described from the Asian genus *Macaranga* (FIALA et al. 1999). This boundary does not reflect a general sharp decline in ant occurrence (BRÜHL, MARYATI & LINSENMAIR 1999), however, a gradual decrease in ant diversity and abundance with altitude is a worldwide phenomenon. Ant-inhabited plants of Neotropical *Cecropia* are regularly found up to 1,500 m, with few exceptional records from 2,000 m (LONGINO 1991b). Obligate plant-ants of the genus *Pseudomyrmex*, although mostly confined to lowland habitats, were recorded from elevations of up to 1,500 m, with only one collection (*P. dendroicus*) from c. 1,700 m (WARD 1989, 1993, 1999). The species of the genus *Tetraponera* known to obligately nest in live stems of their hosts apparently have their upper elevational limit at about 1,200 m (WARD 2001). Similarly, obligate plant-ants of the genus *Myrmelachista* in Costa Rica were mainly collected from low elevational forests but two species occured up to 1,100 and 1,500 m, respectively (LONGINO 2006). To my knowledge, data on altitudinal distribution of ant-plants and their associated plant-ants are limited but it is striking that the information gathered here points to rather similar elevational limit in a narrow band between 1,250 to 1,500 m. It should be noted, however, that most such associations are restricted to lowland areas up to c. 900 m or even lower.

Site conditions (soil quality, light regime, nutrient availability, elevation, temperature, etc) of the host plants were not part of this study but the habitat diversity briefly summarised here indicate that resource availability, both among and within species, is markedly heterogeneous. This heterogeneity, coupled with the specialised use of resources by the plant species, certainly has consequences for the development of ant association and its outcome (DAVIDSON & MCKEY 1993, TRIMBLE & SAGERS 2004). Studies on selected host species addressing the flow of nutrients between plant and ant partner (via associated coccoids) will help to understand the evolutionary dynamics that shape the mutualistic interactions in this system.

4.4.4. Diverse growth forms

As to be expected by the broad taxonomic host range the growth form also differs among host species. The majority of host plants exhibit a tree life form, usually not exceeding a maximum height of about 20 m. However, some host trees such as *Crypteronia griffithii*, *Drypetes fusiformis*, *Neonauclea gigantea*, and *N. longipedunculata* may reach the canopy. Trees growing in the shaded understorey, e.g., *Ryparosa fasciculata* and *Drypetes longifolia*, are not rarely unbranched or branching is confined to a small crown. In contrast, trees growing in sites with open canopy or in clearings, especially *Neonauclea* spp., sometimes gain a shrub-like appearance with many-branched stems. This, of course, has direct consequences for the amount of nesting space offered to the ant partner.

More surprising is the high percentage of the climbing life form among *Cladomyrma* hosts. Five species in the genera *Callerya*, *Luvunga*, *Spatholobus* and *Strychnos* are recorded having associations with *Cladomyrma* ants. They are all woody climbers and, with exception of *Strychnos vanprukii*, show exceptional high occupancy rates by their ant partner. Some lianas, *Callerya* and *Spatholobus*, often reach the canopy in 40 m height but their trailing stems may be much longer. Juveniles of *Luvunga* sp. cannot be recognized as climbers; they grow as unbranched treelets with unifoliolate leaves and straight thorns until they reach a height of at least two meters, only then they become lianescent and produce trifoliolate leaves and recurved thorns. Both life forms are utilized by *Cladomyrma* ants.

Worldwide the liana life form is rare among myrmecophytes. Apart from rattan-palms (*Korthalsia*, *Daemonorops*, *Calamus*), climbers in only seven other genera are known or presumed to be regularly associated with ants: *Canthium*, *Capparis*, *Dichapetalum*, *Poikilospermum*, *Uncaria*, *Vitex* and *Wightia* (BEQUAERT 1922, DAVIDSON & MCKEY 1993, MOOG et al. 2003). Of these, only *Capparis buwaldae* and *Vitex thyrsiflora* have been investigated in some depth (MASCHWITZ et al. 1996, DJIETO-LORDON et al. 2005). Thus the specialisation of either these climbers or inhabiting ants is often not clear. Despite these uncertainties it is obvious that *Cladomyrma* is the dominant coloniser of woody climbers worldwide.

4.4.5. Differences in ant-housing structures

All *Cladomyrma* species nest exclusively in live stems and create their nesting space by excavating the pithy central cavity. Naturally hollow stems are not provided by any host plant (but see *Strychnos* below). However, accessibility, shape, size, location of ant housing structures as well as their appearance during plant ontogeny show some striking differences between host plant species of *Cladomyrma*. The ant-housing

structures can be grouped according to their apparent specialisation for ant occupation. Yet this grouping must be considered provisional because histological studies of stem anatomy of both host plants and their non-ant-associated relatives are needed to detect hidden modifications that might facilitate stem access by specialised ant partners (BAILEY 1922b, TEPE, VINCENT & WATSON 2007a, 2007b)

The **first group** consists of *Cladomyrma* host plants that lack any external sign associated with ant mutualism. The internodes and nodes of *Strychnos vanprukii* are never swollen, neither in juvenile nor mature plants (Fig. 4-82A). Onset of ant occupation occurs earliest in plants 1.5 m long because a minimum stem diameter is necessary for colony-founding ant queens. Each individual plant, prior to ant occupation, usually has two classes of internodes, one in which the pith dries up forming a natural cavity, and one in which the internodes remain solid. The hollow internodes are interspersed between the solid stem sections. Their proportion relative to solid ones increases in larger plants that produce stems with a larger primary diameter. Colony-founding *Cladomyrma* queens apparently do not discriminate between the two internode forms (p. 75). When a plant is inhabited by a *Cladomyrma petalae* colony, the nodal septa of successive internodes are chewed away by the ants. At my study site, however, the proportion of an individual plant occupied was strikingly lower as in other host species utilized by *C. petalae* ants (p. 76 and Tab. 11-1). Also, occupancy rate was the lowest of all hosts included in this study. A prostoma, i.e., a 'weak spot' facilitating ant access into the stem, is obviously not present.

The **second group** consists of host plants whose stems also appear outwardly unmodified (e.g., no hypertrophies to facilitate ant housing). Yet the nodes are slightly or distinctly swollen, the thickening probably being required for support of the large leaves (*Crypteronia*, *Ryparosa*, *Saraca*). The diameter of the stem increases gradually from the internode base to the node. This feature translates into a larger pith canal at the internodal apex and is important during the founding stage, especially in juvenile *Crypteronia griffithii* plants. Here, the primary stem diameter is too small to harbour *Cladomyrma maschwitzi* queens but creation of a founding chamber just below the thickened node allows the early colonisation of young plants (Fig. 4-40). In Borneo and Sumatra, where the small *Cladomyrma maschwitzi* competes for its host with a large *Cladomyrma* species, *C. crypteroniae*, the early colonisation of juvenile hosts gives the former a priority advantage (Fig. 4-41, 4-44). Although there is no distinct swelling of the stems in *Ryparosa fasciculata* and *Saraca thaipingensis* the primary stem diameter of small saplings (i.e., 0.4–1.0 and ≥ 1.0 m in height, respectively) is usually large enough to allow colony-founding. To the naked eye the pith of all plants included in this group appears to be homogenous throughout the internode including

the thickened nodal section. *Ryparosa porcata* and *Saraca dives* have not been studied in the field but examination of herbarium specimens let me assume that their cauline structure is similar to that of their congeners and thus they are incorporated into this group. There is no indication for the presence of a prostoma in any of these plants.

The climber *Luvunga* sp. is somewhat intermediate between the second and the third group. The stem is usually not swollen nor are the nodes thickened, however, small juvenile plants produce swollen internodes which gradually have their diameter towards the node increased (Fig. 4-29). In some cases, the pith of the swollen stem sections appeared slightly softer than the pith of unswollen stem parts. The swollen internodes are short and provide just enough space for a founding chamber of *Cladomyrma*. In plants above 1.5 in height I did not observe such swellings. Due to the scarcity of material I cannot rule out, however, that mature plants occasionally produce hypertrophies in new shoots (compare *Spatholobus* below).

The **third group** includes plants whose stems are partially swollen and where the pith of the hypertrophied stem sections is soft and large-celled. Moderate swellings in *Drypetes longifolia* regularly occur along the stem and usually run over one or two internodes. The pith is heterogeneous, being whitish, soft and large-celled in the swollen stem part (domatium) and comparatively hard and compact in the unmodified stem sections (Fig. 4-51). In juvenile plants the excavated stem cavities are restricted to the large-celled portion of the pith. This patterns suggest that this type of pith facilitates excavation by ants. In adult trees with a larger primary stem diameter, however, the stems are mostly excavated throughout their length, indicating that pith consistency does not prevent a larger *Cladomyrma* colony to hollow out unswollen stem sections. The hypertrophied internodes occur early in plant ontogeny but onset of domatia production appears to differ between the Bornean and Malayan form of *Drypetes longifolia* (p. 102). Although prostomata are not developed, the thickness of the wood is generally smaller at the domatia sections compared to non-dilated parts of the stem.

The nature of ant-housing structures of *D. fusiformis* is a matter of speculation. Field data are lacking and the scarce herbarium material examined indicate that stems lack swollen sections (p. 105). However, secondary growth might have masked slight modifications of stem diameter and/or hypertrophies may be present in juvenile plants only because the primary diameter of mature plants is sufficiently large to allow nesting by *Cladomyrma* ants (as in *D. longifolia*).

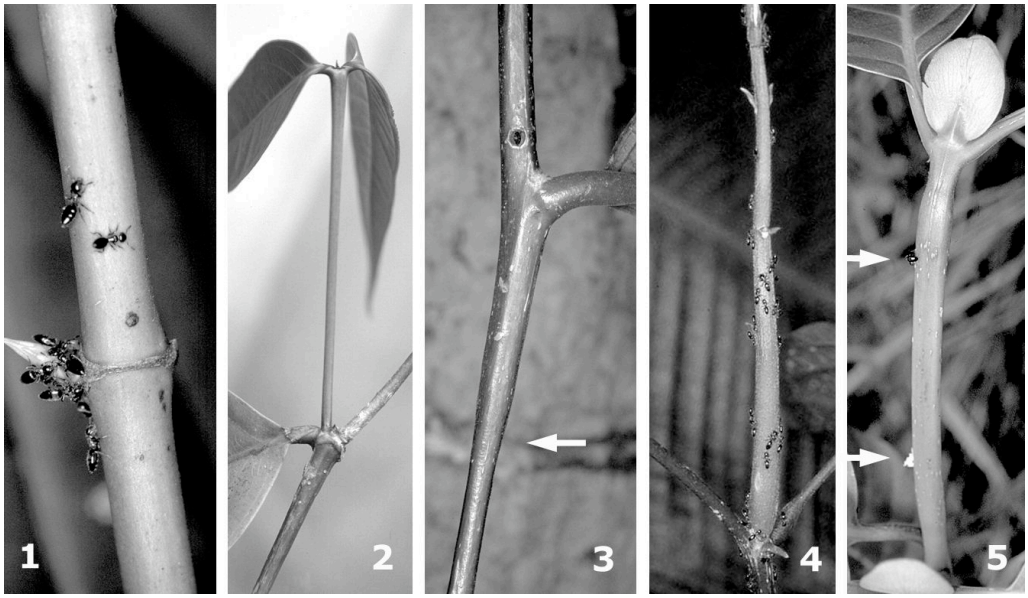


Figure 4-82: Ant-housing structures of *Cladomyrma* host plants (examples), according to the grouping used in the text. **1**: *Strychnos vanprukii* (climber 3.7 m long), stem section with ants; **2**: *Crypteronia griffithii* (juvenile plant 0.8 m in height), young shoot with thickened node; **3**: *Drypetes longifolia* (Malay Pen., tree 3 m tall), twig with swollen stem section and ant entrance hole, arrow indicates begin of hypertrophy which is associated with a sudden change in pith diameter and consistency; **4**: *Spatholobus bracteolatus* (liana >10 m long), young developing swollen shoot patrolled by workers, the swelling gradually decreases with successive internodes; **5**: *Neonauclea gigantea* (sapling), young, moderately swollen domatium with two foundations. Top arrow: a foundress in the process of chewing an entrance hole at the lateral side (prostoma). Bottom arrow: pith remains at an entrance hole where the foundress already entered the hollowed-out chamber. Here, the hypertrophied internode section takes up more than 2/3 of the total internode length.

The **fourth group** consists of woody climbers only and resembles in most aspects the preceding group. The difference to the third group is based on the climbing life form of its members. Because liana saplings typically have very small initial diameters (hence small pith canals), the production of domatia is an important trait to facilitate the colonisation by ants early in the ontogeny of the plant. All three species included here, *Callerya nieuwenhuisii*, *Spatholobus bracteolatus* and *S. oblongifolius*, produce markedly swollen domatia as juveniles. In *S. bracteolatus*, for instance, the increase in stem diameter from a 'normal' internode to the following domatium may exceed three or even four millimeter, in the world of *Cladomyrma* ants a huge improvement concerning nesting space (Fig. 4-14, 4-16). In larger plants the increase in diameter of a newly produced domatium relative to the previous unmodified internode becomes less pronounced but is still a conspicuous feature (Fig. 4-82:4). However, since these climbers continuously increase their diameter with each spurt of growth, the internodes of older lianas become more and more suitable for ant inhabitation. This change in primary stem diameter during plant ontogeny, influencing the amount of stem parts available for nesting, has consequences for the nest structure of inhabiting

Cladomyrma ants. Whereas in young plants occupied domatia are interrupted by sections of small-sized stems containing intact pith (thus forcing the ants to venture on the plant surface before reaching the next domatium), older plants provide sufficiently large stems to allow the ants to create a continuous internal passageway throughout the plant. The pith of domatia is of a soft and large-celled texture and can easily be excavated by the ants. Prostomata are not developed.

Interestingly, the two *Spatholobus* species, although closely resembling each other in vegetative appearance, clearly differ in the formation of their domatia. Whereas the Malayan species, *S. bracteolatus*, has swellings stretching over two (or three) internodes, those of the Bornean species, *S. oblongifolius*, are confined to one internode only. This difference is apparently linked to differences in growth pattern. In each spurt of growth *S. bracteolatus* produces several internodes of which usually the basal two are swollen. In contrast, *S. oblongifolius* produces only a single internode in each pulse of growth. Similar differences have also been observed between domatia of Malayan and Bornean *Drypetes longifolia*.

The **fifth group** includes species of *Neonauclea* only. Domatia of all species occupied by *Cladomyrma* apparently are very similar (although differences in stem structure among species may be uncovered by anatomical studies). They are always produced at the same location. The basal internode of each lateral shoot develops a swelling that stretches over the upper third, half or two third of its total length (the relative and absolute length is variable both among and within species, Tab. 4-4). The vertical main stem axis (the trunk) never produces hypertrophied stem sections and thus is never inhabited by ants. Such a pattern has also been described from domatia of the African ant-plant *Barteria nigritana* (BRETELER 1999, DJIETO-LORDON et al. 2004). Thus, the number of domatia is a function of ramification; the fewer lateral shoots a plant develops the fewer domatia are present. Number of domatia and ant colony size showed a fairly high correlation (Fig. 4-62), although one source of variation, the nest volume of each domatium, was not measured.

In contrast to the ant-housing structures of other host plants of *Cladomyrma*, even in adult *Neonauclea,* a domatium is never connected internally to the next domatium, thus the nest chambers are distributed as separated 'containers' over the tree crown. The pithy central cavity of unmodified 'normal' stem sections is, however, sufficiently large in adult plants to be utilized by the ants as passageway. In a few cases I have observed that *Cladomyrma* ants had enlarged their domatium nest into the adjacent pith canal for several centimeters, suggesting that pith consistency of unswollen stem sections is not a fundamental obstacle for creating a continuous protected nest

gallery. However, the task of excavating the pith up to the next domatium may still be too burdensome in relation to the risk of crossing distances between domatia on the plant surface.

Neonauclea domatia differ in another important trait from the domatia of other host plants. The domatia possess a prostoma, or relatively thin-walled zone where ants gain easy access. It has the form of a straight line running the entire length of the domatium on each lateral side (Fig. 4-57, 4-60). Entrances made by both foundress queens and workers are always found along this narrow lateral band. The pith of the domatia is whitish and soft but does not dry up as in extra-Bornean *Neonauclea* ant-plants which are inhabited by *Crematogaster* ants (Fig. 4-59). Observations of complete foundation processes are limited, but founding queens of *Cladomyrma dianeae* appeared to create a founding chamber in *Neonauclea* domatia, on average, in approximately half the time than foundresses of *C. petalae* colonising unmodified internodes of *Saraca thaipingensis* (1-2.5 h and 2-4 h, respectively). Although size of *C. dianeae* foundress queens is slightly smaller than those of *C. petalae* I cannot rule out that *C. dianeae* foundresses have greater resources available for the excavation process. The observed difference in domatia access time, however, is likely enhanced in *Neonauclea* by the provisioning of a prostoma and soft pith.

As summarised here, hosts of *Cladomyrma* are heterogeneous in terms of descent (broad range of unrelated taxa), distribution, habitat, growth form and ant-housing structures. The latter includes unmodified stems (*Strychnos*), thickened nodes in otherwise unmodified stems (*Crypteronia*, [*Luvunga*], *Ryparosa*, *Saraca*), swollen internodes with heterogeneous pith (*Drypetes*), a trait which is especially pronounced in some juvenile climbers (*Callerya*, *Spatholobus*), and strongly swollen internodes characterised by soft, large-celled pith and a prostoma (*Neonauclea*). [Detailed information on the recently discovered host, *Sphenodesme*, is, at present, lacking.] Despite these differences, host species share common traits that are important in relation to ant association.

4.4.6. Preadaptations for myrmecophytism

In the context of the differences at various levels, certain similarities between hosts are striking. On host generic level, a common myrmecophytic ancestor can be ruled out. Instead, it is highly plausible that repeated events such as host expansion and host switching, or the secondary exploitation of preexisting ant-plant mutualism, has produced the pattern of *Cladomyrma*-host relationships observed today. Shared features thus might help to identify structures that could function as prerequisites for the selection of a host by *Cladomyrma*.

Common features of *Cladomyrma* host plants, shared by all species, are 1) the location of ant-housing structures in stems; 2) the lack of a long, erect pubescence on stems, domatia or leaves; 3) the lack of ant rewards such as food bodies or extrafloral nectaries (but see *Saraca* and *Ryparosa* below); and 4) the suitability as a substrate for phloem-feeding, ant-associated coccoids. Do these traits combined provide the necessary 'starting material' for becoming a host of a plant-ant such as *Cladomyrma*?

Generally, structures for housing ants are extremely variable ranging from hollow (fistulose) stems over shelter-forming leaves and persistent stipules to inflated hypocotyls (chambered tubers) or spine galleries, with each type represented by morphologically diverse examples (HUXLEY 1986, JOLIVET 1996). Worldwide, the largest group of myrmecophytes, however, is that in which domatia are located in stems (DAVIDSON & MCKEY 1993). This is also true when tropical regions in the New and Old World are considered separately (BENSON 1985, BEQUAERT 1922, MOOG et al. 2003). Reasons to account for the prevalence of cauline domatia among ant-plants are certainly their relative longevity and seclusion. A recent study on the petiole chambers in *Piper* sect. *Macrostachys* demonstrated that the critical plant characters determining inhabitability by ants include persistency of the petiolar margin and the tendency for the petiole to form a closed chamber (TEPE, VINCENT & WATSON 2007b). What plant traits then may have facilitated the production of stem cavities that could be transformed by selection into specialised structures for housing ants?

A hypothesis proposed by WARD (1991) states that occasional inhabitations of live, insect-bored cavities may be crucial to the inception of more specialised interactions with plants. Together with cavities formed by spontaneous drying of pith canals, these cavities provided ants with a long-lived and protected nest site. When the presence of ants conferred a net benefit (protection against phytophagous insects, including wood-borers), selection acted on the plant to evolve traits facilitating its occupancy by ants. Increasing evidence supports WARD'S hypothesis that ant-plant symbioses have evolved from casual and opportunistic relationships between plants and ants. Stem-boring insects commonly pave the way for subsequent colonisation of live stem cavities by opportunistic ants. Examples are recorded from tropical Africa (*Cuviera*; BEQUAERT 1922), the Neotropics (e.g. *Acacia*, *Avicennia*, *Clibadium*, *Remijia*, *Tachigali*, *Tecoma*, *Witheringia*; BAILEY 1923, BENSON 1985, HUXLEY 1986, NESOM & STUESSY 1982, WARD 1991, WHEELER 1942), Southeast Asia (*Acacia*, *Archidendron*, *Chisocheton*, *Clerodendrum*, *Gigantochloa*, *Leptospermum*, *Uncaria*; PIJL 1955, WEIR & KIEW 1986, MOOG et al. 2003), and Australia and New Guinea (*Avicennia*, *Eucalyptus*, *Syzygium*, *Timonius*; GULLAN, BUCKLEY & WARD 1993, SANDS & HOUSE 1990, WARD 1991).

One prerequsite for ants utilising natural hollow or hollowed-out stems is that they must provide sufficiently large dimensions to support the reception of founding queens and colonies (MOOG et al. 1998, this thesis). A plant trait that likely acted as a predisposition to evolve association with ants are thus thick stems and twigs (DAVIDSON & MCKEY 1993). Because a large primary stem diameter (before secondary growth) is associated with a large pithy central section, *"thick-twigged plants offer greater opportunities than do thin-twigged taxa for wood-boring insects, and for ants which nest secondarily or primarily in the cavities of plants"* (DAVIDSON & MCKEY 1993, p. 20). Studies showed the existence of a generally strong relationship between twig cross-sectional area (before secondary growth) and surface area of leaves borne by it; vascular supply and mechanical support being the predominant factors for the observed leaf-stem size correlation (WHITE 1983, BROUAT et al. 1998). This correlation means that selection acting on leaf size could also drive change in stem diameter (BROUAT & MCKEY 2000).

Within host species of *Cladomyrma* I have repeatedly observed that stem primary diameter increases over plant ontogeny (a general feature of plants; BROUAT et al. 1998), and that onset of ant occupation is dependent on a minimum size of stems. Thus some hosts are colonised at an earlier stage than others. Species of *Crypteronia*, *Ryparosa* and *Saraca* ('second group') do not provide swollen stems but produce relatively large-sized internodes and thickened nodes. These species are characterised by having comparatively large leaves (in *Saraca* also compound), typical for many plants of humid and shaded environments. Also, these hosts produce larger leaves than most of their congeners. Onset of ant occupation usually occurs in saplings between 0.5–1.0 m (*Crypteronia*, *Ryparosa*), and 1.0–1.5 m (*Saraca*) in height, thus ant occupancy, even in the absence of swollen domatia, occurs at a relatively early stage of development. [In *Strychnos*, a climber with unmodified stem and comparatively small leaves, onset of ant colonisation was observed to occur from a plant length of 1.5 m onwards.]

If larger leaves, and thus thickened support structures, are related to habitat, slow-growing plants of moist, shaded habitats and fast-growing plants of early successional environments may have frequently give rise to regular ant association (DAVIDSON & MCKEY 1993). Such a scenario is supported by the high frequency of myrmecophytes with cauline domatia recorded from both habitat types: for example, African *Leonardoxa*, Malesian *Alectryon*, *Aphanamixis*, *Chisocheton*, *Harpullia*, *Kibara*, *Myristica*, *Sarcopteryx*, *Steganthera*, and, of course, the well-known pioneer trees of Neotropical *Cecropia* and Malesian *Macaranga* and *Endospermum*. Other examples

from riverine disturbances or forest light gaps are African *Barteria* and *Vitex*, and Neotropical *Triplaris* (list not exhaustive).

The *Cladomyrma* hosts in the genus *Neonauclea* fall into the latter category of pioneer plants and plants of riverine and forest light gaps. Onset of ant occupation is linked to first branch height because domatia are produced only on lateral shoots. First domatia appeared in heights of 0.3 to c. 1.2 m. This appears to be in contrast to many large-leaved light-demanding species (both myrmecophytic and non-myrmecophytic) that are often characterised by a large first branch height (KING 1998). This delay of branching in pioneer species allows them to support a considerable leaf surface area with a minimum investment in woody framework (WHITE 1983). However, other light-demanders such as the wide-spread tropical genus *Trema* initiate branches at a low height (KING 1998). Branched saplings can expand laterally and direct this lateral growth preferentially into areas of higher light. In addition, early branching in *Neonauclea* ant-plants is expected to be advantageous because it is coupled with early ant colonisation, hence a protective effect on leaves and meristems. Under unfavourable conditions (low light), however, *Neonauclea* ant-plants appeared to delay first branching, perhaps indicating that the trait 'growth for light' competes with the trait for 'domatia formation' (ant protection). Comparative studies on saplings of light-demanding myrmecophytes with initial different location of domatia (i.e., main stem versus lateral shoots) are necessary to better understand onset of first branching and its evolutionary implications.

4.4.7. Evolutionary specialisation of ant-housing structures

BROUAT & MCKEY (2000) postulated that expression of domatia later in development is the primitive condition in lineages with domatia, and that increasing specialisation of ants and plants enhanced both the probability of establishment and ant protection, favouring precocity of onset of domatia. Whereas this scenario is plausible, it does not mean that present-day patterns of ant/host associations represent the evolutionary pathway of specialisation within a lineage of ant/plant mutualism. For example, morphologically 'transitional' myrmecophytic species in the genus *Macaranga* section *Pruinosae* have pithy domatia that must be excavated by *Crematogaster* (*Decacrema*) ants, and onset of domatia formation occurs later in plant ontogeny than in sympatric species of section *Pachystemon* which have naturally hollow stems (FIALA et al. 1999). Although the *Pruinosae* mutualisms appear to be evolutionary predecessors of those of *Pachystemon*, a recent phylogenetic study suggests that the association originated in *Pachystemon*, and that *Decacrema* ants later expanded onto *Pruinosae* while retaining their *Pachystemon* hosts (QUEK et al. 2004).

Most *Cladomyrma* host plants are unrelated, demonstrating that myrmecophytism in this system must have multiple independent origins. Any grouping of the hosts according to their increasing specialisation to facilitate early colonisation by the ant mutualist is thus purely artificial and does not reflect phylogenetic histories. It provides, however, evidence for potential evolutionary routes that may have led to more intimate relationships between *Cladomyrma* ants and their host plants (provided that the ant-housing organs evolutionary specialised in the presence of *Cladomyrma* and not in association with an unknown mutualist which was later replaced by *Cladomyrma*).

Overall, the ant-housing structures of *Cladomyrma* host plants apparently show different degrees of specialisation, including three main traits that are known to directly influence excavation of cauline domatia by ant mutualists, i.e., stem diameter, pith texture and entry points (prostomata) (BAILEY 1922b, BROUAT & MCKEY 2000, TEPE, VINCENT & WATSON 2007a).

Stem size: As I have stressed earlier, there is a minimum primary stem diameter (varying with the ant species) below which a cavity cannot be inhabited by a foundress ant, and the onset of a given association thus occurs either early or comparatively late in plant ontogeny. In some hosts stem sections utilised for ant-housing do not appear outwardly modified (*Strychnos*) although the nodes are often moderately to distinctly enlarged relative to the adjacent internodes (*Crypteronia*, *Ryparosa*, *Saraca*). Whether the increase in node dimensions is due to constraints on leaf support (e.g. vascular supply, mechanical stability) or already an adaptation to ant occupation is open to speculation. In all *Cladomyrma* hosts with thickened nodes, however, expansion of the pith in nodal regions contributes to the enlargement of the nodes. This in turn provides more nesting space for queens which often to regularly excavate their founding chamber close to the nodal region. Other hosts of *Cladomyrma* produce slightly to conspicuously swollen stem sections (*Drypetes*, *Neonauclea*), and these plants are usually colonised at earlier stages of development than hosts lacking such hypertrophies. The cauline domatia offer clear support for evolutionary specialisation, especially because the production of such structures is evidently costly to the plant. For example, costs of domatia production, especially in juvenile plants, consists of additional tissue investment to ensure mechanical stability and to protect mutualistic ants from predation (BROUAT & MCKEY 2001, MOOG et al. 2002). The latter factor, myrmecophagy, occurs in many ant-plant systems and appears to represent an important cost of myrmecophytism (FEDERLE et al. 1999).

For woody vines the onset of ant occupation is particularly difficult to establish early in plant ontogeny. They typically have very small initial stem diameters and, after

passing through an upright seedling stage, lianas rely on other plants for physical support. Also, in comparison with trees, liana stem diameter growth rates are very low (PUTZ 1990). Climbers associated with *Cladomyrma* solve this problem by producing strongly swollen cauline domatia (*Callerya*, *Spatholobus*) filled with soft pith early in their ontogeny. In later developmental stages the primary stem diameter eventually increases and hypertrophies of new shoots become less and less pronounced. Prior to this study these domatia have never been recorded because collectors of botanical specimens usually ignore plant individuals in the non-reproductive stage.

Pith: Generally, pith functions in mechanical support in young shoots and in storage. It is typically homogeneous in non-monocotyledonous angiosperms, usually with a slight increase in cell size towards the center. However, a common feature of many myrmecophytes with stem domatia is heterogeneous pith, e.g., *Barteria, Cordia, Endospermum, Leonardoxa, Macaranga, Myristica*, *Vitex* (WARBURG 1897, BAILEY 1922b, 1924, SCHAEFFER 1971, MCKEY 1984, FIALA & MASCHWITZ 1992a). Swollen stem sections typically differ from unswollen stem parts by being large-celled, whitish and soft. In many ant-plants, the pith of hypertrophied parts of the stem dries up spontaneously, leaving a naturally hollow chamber, e.g., *Capparis, Clerodendron, Duroia, Ficus, Humboldtia, Myrmeconauclea*, *Tetrathylacium* and *Zanthoxylum* (SCHUMANN 1888, TENNANT 1989, MASCHWITZ et al. 1989, 1994, 1996a, MASCHWITZ, FIALA & LINSENMAIR 1992, 1994, KROMBEIN et al. 1999).

Heterogeneity of the pith is also a common trait among *Cladomyrma* host plants (*Callerya*, *Drypetes*, *Neonauclea*, *Spatholobus*), pith degeneration, however, is absent. In hosts with stem sections containing soft pith *Cladomyrma* queens restrict their colony founding to these modified stem parts, but, as a rule, the intial nest chamber is later expanded by the ant workers into stem sections with unmodified pith, at least in associations where the colony and its host have reached a certain size (*Neonauclea* is an exception to this rule). Furthermore, colony-founding ants colonising *Neonauclea* excavate their initial nest chamber in about half the time than those entering unmodified stems of *Saraca*. This pattern suggests that the modified pith itself –and not only the associated enlarged stem diameter– facilitates excavation by foundress ants. [But prostomata of *Neonauclea* may further reduce the time needed for chewing into the stem.]

Less obvious modifications of the pith may be present in stems lacking hypertrophies. A recent study of stem anatomy by TEPE, VINCENT & WATSON (2007a) revealed novel modifications in *Piper* ant-plants of section *Macrostachys*. Colony initiation takes place in the petiole domatia of *Piper* but the ants chew a hole into the outwardly unmodified

stem from the petiole cavity and excavate the stem to create cauline domatia. Prior to excavation by ants, stems of myrmecophytes were characterised by strongly heterogeneous piths in which a large, central area had relatively large cells lacking intracellular styloid crystals (raphides) and starch grains with a periphery of smaller cells containing numerous crystals. In addition, medullary vascular bundles (MVBs) are confined to the periphery of the pith. The nest cavity excavated by the ants was always restricted to the large-celled region. This combination of traits was only found in the four species regularly inhabited by the ant mutualist, *Pheidole bicornis*. In contrast, generalised myrmecophytic and non-myrmecophytic *Piper* species have dense pith (with only few large pith cells), scattered MVBs, and the needle-shaped crystals are present in abundance throughout the pith. The crystals possibly function as a deterrent to excavation. Preliminary phylogenetic evidence suggests two to four independent origins of specialised myrmecophytes in section *Macrostachys* (TEPE, VINCENT & WATSON 2004), thus indicating parallel evolution in several lineages of *Piper* on the same suite of stem traits. Anatomical studies are required to determine whether similar stem features also characterise ant-excavated tissues of *Cladomyrma* host plants, especially those with no or slight outward stem modification such as *Crypteronia*, *Ryparosa* and *Saraca*

Prostoma: A key adaptation of plant-ants inhabiting stems of myrmecophytes is the capacity to chew entrance holes into domatium walls. In ant-plant research a true prostoma is defined as a preformed thin zone of the stem, often lacking vascular or other lignified tissues, where ants preferably chew their entrance holes (IHERING 1907, BROUAT et al. 2001). Examples are New World *Cecropia* (DAVIDSON et al. 1991), African *Leonardoxa* (MCKEY 1984) and Asian *Macaranga* (FEDERLE et al. 2001). The latter authors list several possible benefits of a prostoma to the ants, including 1) facilitation of colony foundation, 2) prolongation of the time window for colonisation, 3) cost reduction for adult ant colonies, 4) minimising plant damage caused by entrance holes, and 5) selective filter against generalist ants.

The domatia of *Neonauclea* ant-plants possess a prostoma that runs along the entire length of each lateral side of the domatium (Fig. 4-60). The thin-walled straight lines are maintained throughout plant ontogeny and serve as prostomata for ants which preferentially chew their entrance holes at these positions. The lateral thin zones are not present in unswollen stem parts, suggesting that they have an adaptive value in the ant/plant mutualism. However, studies on stem anatomy to clarify, for example, the distribution of lignified tissue (vascular elements and the sclerenchymatous cylinder) as well as the position of the prostomata in relation to phyllotaxy have yet to come. Thus it is at present premature to draw firm conclusion on the possible benefits of the

prostomata to the ants. Nevertheless, *Cladomyrma* founding queens were never observed to chew an entrance hole outside the thin-walled line; the ability to recognise prostomata is generally thought to be a specialised trait of plant-ants (DAVIDSON & MCKEY 1993). In *Neonauclea* the lateral thin zones at the domatium appear to extend the time window of colonisation. Secondary growth is obviously both delayed and reduced at the prostoma position, and I actually observed foundress ants successfully entering domatia that were at least several months old (n=3).

4.4.8. The special case of *Neonauclea* and its sister taxon *Myrmeconauclea*

Neonauclea is the only host genus of *Cladomyrma* in which a considerable radiation of myrmecophytic species has occured. Do we find increasing domatium specialisation in this lineage? Of the 17 myrmecophytes eight are restricted to Borneo, six to Sulawesi, two to Sumatra, and one to the Philippines (Fig. 4-55). In contrast, the 48 non-myrmecophytic *Neonauclea* species together have much larger geographic ranges in comparison with the 17 myrmecophytes (RIDSDALE 1989). Such more restricted distribution patterns could be taken as indication of a monophyletic origin of the ant-*Neonauclea* associations. Interestingly, the endemic Bornean, Sulawesian and Sumatran myrmecophytic *Neonauclea* species, respectively, are inhabited by distantly related ant species. At present, four *Cladomyrma* species are known to colonise the Bornean myrmecophytic *Neonauclea* (this study), whereas the extra-Bornean species are all inhabited by specialised *Crematogaster* species belonging to the subgenera *Physocrema* (Sumatra) and *Decacrema* (Sulawesi) (MASCHWITZ & FIALA 1995; own observation). [The subgenus inhabiting *Neonauclea* in the Philippines has not been established.]

The structures of the swollen internodes are different in *Neonauclea* species inhabited by *Cladomyrma* and those colonised by *Crematogaster* plant-ants. In the former, they are formed by an internode expansion containing soft pith that has to be excavated by the ants. In the latter, however, the internode expansion becomes hollow as a result of the disintegration of the pith prior to ant colonisation (Fig. 4-59). These two highly specific morphologies of the swollen internodes of the Bornean, Sulawesian and Sumatran myrmecophytic *Neonauclea*, respectively, might indicate monophyletic origins of these structures, which have independently been exploited by the different ant taxa. However, there are no obvious clearly defined differences between domatia morphology within each group (unpublished results). Comparative anatomical studies are needed to test whether the apparent morphological homogeneity of *Cladomyrma*- and *Decacrema*- or *Physocrema*-inhabited domatia, respectively, can be supported.

Myrmeconauclea strigosa (Korth.) Merrill, known from the islands of Palawan and Borneo, is a rheophytic shrub or small tree associated with ants living in hollow stem swellings (WINKLER 1910, MERRILL 1920). The small-sized domatia become hollow by pith degeneration and they spontaneously develop slit-like openings that give access for a variety of tree-dwelling ants (MASCHWITZ et al. 1989). In several localities, *Crematogaster* ants are the dominant associates but all these species appear to be non-specific to its host (own unpubl. results). Contrary to the observations recorded in DAVIDSON & MCKEY (1993, p. 35), the ant inhabitants often tend trophobiotic coccids on the plant surface (stem, flower buds and fruits) as well as inside the domatia. Nevertheless, the ants sometimes leave their host to forage. Some *Crematogaster* species are capable of biting additional holes into the domatia wall and I once even observed that a colony had enlarged all their domatia cavities by chewing short tunnels (1–1.5 cm) into the adjacent unswollen stem sections.

To summarise, *Myrmeconauclea* provides a third type of ant/plant symbiosis in the tribe Naucleeae. Compared to the two types of *Neonauclea* mutualism with plants-ants of the genera *Cladomyrma* (Borneo) and *Crematogaster* (Sulawesi, Sumatra, Philippines), important differences are the absence of specialist plant-ants and the provision of preformed entrance slits. The assumed close phylogenetic relationship of *Myrmeconauclea* with *Neonauclea* (RIDSDALE 1978) raises the question whether the acquisition of myrmecophytism is monophyletic, although myrmecophytism in *Myrmeconauclea*, Bornean *Neonauclea* and extra-Bornean *Neonauclea* appears not to be homologous.

In a recent phylogenetic study, based on nuclear ribosomal DNA internal and external transcribed spacer sequences (ITS, ETS), we support –in agreement with morphological data– the monophyly of both *Neonauclea* and *Myrmeconauclea* (RAZAFIMANDIMBISON et al. 2005). Our analyses further suggest that myrmecophytism of Bornean myrmecophytic *Neonauclea* has multiple origins, despite the seemingly homologous domatia and the small group of specialist plant-ant associates of the genus *Cladomyrma*. Unfortunately, we were unable to draw any conclusions regarding the evolution of ant–*Neonauclea* associations on Sulawesi and Sumatra, as our study included only one myrmecophytic *Neonauclea* species from each island.

Furthermore, we interpret the low level of variation in both the ETS and ITS sequence data as indication of a recent and rapid radiation for *Neonauclea* and a recent and slow radiation for *Myrmeconauclea*, because these sister genera have unbalanced species richness (65 and 3 species, respectively). Differences in species diversities of sister groups can indicate disparities in their diversification rates (HODGES 1997). We

postulate that the diversification of *Neonauclea* in Southeast Asia is not predominantly due to the acquisition of myrmecophytism but likely associated with the nature of its fruits containing small wind-dispersed seeds and its ability to colonise a wide range of habitats. In contrast, we argue that the acquisition of new morphological traits (pseudo-multiple fruits and long-tailed seeds) has allowed *Myrmeconauclea* to specialise on rheophytic habitats and, in turn, its narrow ecological tolerance may have hindered its speciation (RAZAFIMANDIMBISON et al. 2005).

Indirect support for this scenario comes both from the non-monophyly of the Bornean myrmecophytic *Neonauclea* and the similarity in the nucleotide substitution rates of the sampled myrmecophytic and non-myrmecophytic *Neonauclea*, indicating that the acquisition of myrmecophytism could not have been the key innovation (sensu HEARD & HAUSER 1995) responsible for the radiation of myrmecophytic *Neonauclea*. Our study, however, generally suffers from the poor taxon sampling of non-myrmecophytic *Neonauclea* species, thus further work is required to evaluate the hypotheses of the evolution of myrmecophytism in the *Myrmeconauclea–Neonauclea* clade. Plus, ambiguity in placement of some *Neonauclea* species suggests that additional sources of phylogenetically informative characters are needed.

Although our limited sampling of the non-myrmecophytic *Neonauclea* species prevented us from performing a molecular clock test or assessing diversification rates, the study of QUEK et al. (2004, 2007) on the phylogeny of *Crematogaster* (subgenus *Decacrema*) provides estimates on the split between *Decacrema* ants inhabiting myrmecophytic *Macaranga* in western Malesia and those colonising *Neonauclea* east of Wallace's line in Sulawesi. Their calculation of the *Decacrema* chronogram indicates that the split occurred between 22.6 to 15.9 million years in the early or middle Miocene, thus placing the split into a time where a perhumid climate, a prerequisite for the *Decacrema*/plant association, became well established in the region from about 20 Ma onwords (MORLEY 2000). The timeline applied to the *Decacrema* phylogeny also concurs with other independent biogeographical events reconstructed from palynological data, thus suggesting that the evolutionary histories of *Decacrema* and their *Macaranga* hosts are at least 12 million years old (QUEK et al. 2004). It is, however, not known whether the ancestors of Sulawesian *Decacrema* had already established an association with *Neonauclea* or other ant-plants.

Centres of *Neonauclea* diversity are not clearly defined, with 14 species in Borneo, 12 in the Philippines, 11 in Sulawesi and 20 in New Guinea (Fig. 4-55). This is suggestive evidence for an early dispersal of *Neonauclea* progenitors in the Malesian region. Arrival of *Neonauclea* ancestors on Sumatra (six species) may have occurred in

younger times. In contrast, centres of diversity of myrmecophytic *Neonauclea* are strictly confined to Borneo and Sulawesi, with eight and six species, respectively. This corresponds with the two different lineages of plant-ants (*Cladomyrma*, *Decacrema*) that associate with the geographical disjunct *Neonauclea* species. The Sumatran species of myrmecophytic *Neonauclea* also appear to have been independently colonised by *Physocrema* ants; except for the full pith degeneration, a trait associated with *Crematogaster* ant partners, several other domatium features of Sumatran *Neonauclea* species are closer to those of Bornean than Sulawesian species (Tab. 4-5). The features characterising the ant/*Myrmeconauclea* relationship point to yet another independent origin of myrmecophytism.

The diversity of myrmecophytic characters in the *Myrmeconauclea*-*Neonauclea* clade strongly contrasts with the low molecular variation, a discrepancy that is also recorded from *Macaranga*, a genus with a substantial radiation of myrmecophytes (BLATTNER et al. 2001, DAVIES et al. 2001, BÄNFER et al. 2006). In addition, their studies provided no evidence that myrmecophytic traits underwent sequential change through evolution; self-hollowing domatia (*Pachystemon* group of *Macaranga*) evolved independently from ant-excavated domatia (*Pruinosae* group). Mapping myrmecophytism on phylogenetic trees of *Macaranga* indicated that the trait evolved independently between two and four times and was lost between one and three times (BLATTNER et al. 2001, DAVIES et al. 2001).

The general outcome of recent studies on ant/plant associations is that similar mutualisms often evolved independently, and host expansion, host switching and secondary exploitation within established mutualistic systems appears to be common (WARD 1993, AYALA et al. 1996, LONGINO 1996, YU & DAVIDSON 1997, BROUAT et al. 2001, FELDHAAR et al. 2003b). All evidence available for the ant/*Neonauclea* mutualism paint a similar picture but detailed phylogenetic studies on both ants (*Cladomyrma*, *Decacrema* and *Physocrema*) and *Neonauclea* plants is required to better understand the evolution of myrmecophytism in these lineages.

5. Host-choice

5.1. INTRODUCTION

While most *Cladomyrma* species appear to have a restricted host range, that of the genus as a whole is broad. Host affiliation shows considerable variation both at plant species and genus level (Tab. 11-1 Fig. 11-1 e.g., ant species/plant genus pairings range from 1:1 for *Cladomyrma maschwitzi* (*Crypteronia*) to 1:6 for *C. petalae* (*Saraca*, *Spatholobus*, *Drypetes*, *Ryparosa*, *Luvunga*, and *Strychnos*). The latter species has a very broad host plant spectrum, comprising unrelated host species from five different families. At Fraser's Hill, Malay Peninsula, five host plant species occur sympatrically in a narrow elevational band at 800 m a.s.l. (*Drypetes*, *Luvunga*, *Ryparosa*, *Saraca*, *Spatholobus*). Along one transect of only 50 m these hosts were all found to be inhabited by *C. petalae*.

This surprisingly broad host spectrum poses a distinct adaptive problem. What are the signals involved in host-finding and host-choice by founding ant-queens? It appears highly unlikely that these unrelated hosts possess similar scent profiles differentiating them against a diverse background of plants. It could be argued that *Cladomyrma petalae* is a 'jack-of-all-trades', colonising any suitable plant in the vicinity of its natal host. Localisation of hosts would then be independent of taxon, instead the detection of host could be determined by general traits such as age of plant tissue and internode size only. Unspecific volatile organic compounds emitted by young plant tissue may act as a general signal to foundress queens of *Cladomyrma petalae* (DICKE 2000, MÜLLER & HILKER 2000, PICHERSKY & GERSHENZON 2002).

This scenario, however, is not the case. Although I cannot rule out that host range might be still more diverse than is currently known, both observations in the field and the examination of nearly 5,000 herbarium specimens of congeneric host taxa indicate that host plants are not unspecifically selected by the ant queens.

Under these circumstances, which mechanisms are involved in the restriction of *Cladomyrma petalae* to only a few, unrelated hosts? Host-choice may be based on a learned odor profile. Foundress ant queens search for individuals of the plant species in which they were raised. In the obligate ant-plant system *Barteria-Tetraponera* it has been demonstrated that experience gained during the larval and nymphal stages as well as during the first part of adult life had a (weak) effect on nest plant selection by ant workers (DJIETO-LORDON & DEJEAN 1999). However, innate attraction of *Tetraponera aethiops* workers to the host *Barteria fistulosa* remained strong, even

when workers were raised in the presence of non-*Barteria* test plants. The authors conclude that under natural conditions the influence of the environment reinforces innate attraction.

> Methodological problems make bioassays for testing host-choice of plant-ant queens notoriously difficult. First, it is impossible to use naïve queens for studies, because they cannot be raised apart from their hosts. Second, it is almost impossible to catch alate queens directly after mating but before colony-founding. Even when successful the natal host would then be unknown. Third, the use of virgin alate queens collected from the natal host *prior* to the nuptial flight may result in non-natural responses due to lack of insemination or other possible cues (e.g., flight distance before colony-founding). Fourth, queens may be collected during the process of colony-founding but these queens have already shed their wings. When used in an experiment they have a reduced mobility and thus are probably under pressure to make a choice even if the host plant candidate appears less suitable. Furthermore, collecting colony-founding queens will only produce a low sample size due to the high search effort. Lastly, nulliparous queens (that have not yet laid eggs) can be collected from internodes of freshly colonised plants (e.g., INUI et al. 2001) but the previous and presumably exhaustive task of colony-founding may influence the subsequent behaviour of the queens in host-choice experiments in unknown directions.

Considering the methodological problems involved in bioassays on host-choice I decided to test whether foundress queens of *Cladomyrma petalae* accept other sympatric hosts or non-host plants. Are the queens capable of accepting sympatric hosts despite their phylogenetic distance to the source plant? Are they forced to enter non-host species when having no choice? In a wider context: What is the level of plasticity in the choice of the supporting plant? Is there a potential for shifting to new hosts on an individual level?

In the following, I will present some preliminary results of no-choice tests on host acceptance by *Cladomyrma petalae* queens.

5.2. MATERIAL AND METHODS

The test were conducted using branches (n=21) with young internodes and suitable stem diameter of six different plant species known to be hosts of *Cladomyrma petalae*. Branches with fresh domatia of an allopatric ant-plant from Sumatra, *Neonauclea cyrtopoda*, served as control (n=10). A bushy tree was kept in a greenhouse at the study site in Ulu Gombak, West-Malaysia. *N. cyrtopoda* is regularly inhabited by an obligate *Crematogaster* species and thus generally suitable for ant-inhabitation. I do

not expect it to possess hidden traits deterring ants. The latter holds true for the sympatric, non-specific ant-tree *Pometia pinnata* forma *glabra* (MOOG et al. 2008). Young branches were also used in the bioassay as controls (n=4).

Foundress queens of *C. petalae* in the process of colony-founding (gnawing a hole into the stem) were searched and collected from plants of *Saraca thaipingensis*, *Spatholobus bracteolatus* and *Strychnos vanprukii* (source plants). All these queens had already shed their wings.

The test branch was placed upright in the middle of a plastic box surrounded by water, preventing the queens to leave the arena. Then, a foundress queen was introduced at the apex of the branch. The behaviour of each queen was monitored for one hour. A plant was considered as 'accepted' when the queen had clearly left a deep mark on the plant surface by chewing.

Gnawing a hole into the stem is the last step in the process of host-selection behaviour (Fig. 5-1). Foundresses that did not show any sign of the typical stereotyped founding behaviour during the observation period were placed back onto the source plant. If, then, the queen accepted the original source plant I considered the previous rejection as valid. However, if a queen did not return to normal foundation behaviour on the source plant the rejection of the former plant was considered invalid and the data were omitted from the analysis. This design reduces effects on queen behaviour by handling or other possible disturbances. Each queen was tested only once.

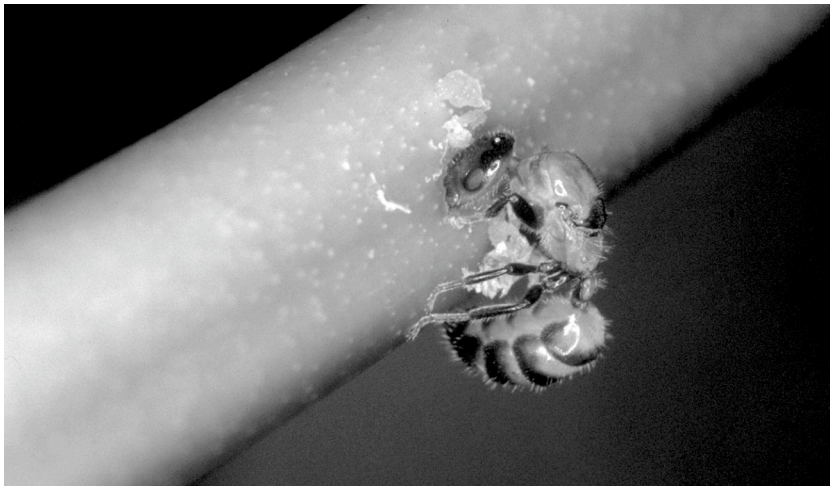


Figure 5-1: Colony-founding by *Cladomyrma petalae*. A dealate queen chews a hole into a young internode of *Saraca thaipingensis*.

5.3. RESULTS

The results are summarised in table 5-1. Foundress queens of *Cladomyrma petalae* accepted one third (7 of 21 trials) of the offered sympatric host-plants, whereas control plants were always refused (0/14). The difference between sympatric hosts and controls is significant (Fisher's exact test, *P* = 0.0272, *df* = 1, chi square 5.833).

A more detailed analysis of the data would reveal that several typical steps in the host-selection behaviour [1] of *Cladomyrma* were observed in the test plants of sympatric hosts – even if they were not accepted within the observation period of one hour. These behavioural responses (see footnote step ii or iii to v) of the queens were usually not observed in the controls. Moreover, it should be noted that a certain percentage of 'correct' host plant species is rejected even under natural conditions. In the field I noticed three winged queens which, after a thorough inspection of young *Saraca* stems (taking 2–14 min), flew off and continued their search.

Table 5-1: Host-acceptance experiment with queens of *Cladomyrma petalae* (no-choice test). Foundress queens collected during the founding process from source plants were introduced to young branches of sympatric hosts and controls. Given are numbers of accepted plants; total number of tested plants in parenthesis (). For details see text.

source plant: / **experimental plant**	*Saraca thaipingensis*	*Spatholobus bracteolatus*	*Strychnos vanprukii*
sympatric hosts:			
Saraca thaipingensis		1 (4)	1 (1)
Spatholobus bracteolatus	2 (3)		
Strychnos vanprukii	1 (3)		
Ryparosa fasciculata	0 (4)		
Luvunga sp.	0 (3)		
Drypetes longifolia	2 (3)		
pooled:	**7 (21)**		
controls:			
Neonauclea cyrtopoda	0 (6)	0 (4)	
Pometia pinnata	0 (4)		
pooled:	**0 (14)**		

[1] These steps include: (i) running in a more or less straight line up and down the internode; (ii) changing to a sinusoidal running curve, thereby encircling the internode from time to time, sometimes entering the adjacent leaf but returning to the stem; (iii) stopping now and then for several seconds to inspect a spot on the internode; (iv) slowing down the movements and extending the inspection time of stem spots, typically accompanied by antennating, palpating and test biting; (v) gnawing a hole into the stem (see also MASCHWITZ et al. 1991).

5.3.1. Summary of the results: host-choice

- queens of *Cladomyrma petalae*, a species with a taxonomically diverse host range, can accept sympatric hosts when having no choice
- plants not belonging to the 'usual' host spectrum are not accepted

5.4. DISCUSSION

This study suggests that foundress queens of *Cladomyrma petalae* possess some plasticity in host-choice. Under experimental conditions queens can be 'forced' to shift to other plants of their 'usual' host spectrum despite their phylogenetic distance. Non-host plants appear to be consistently refused but sample size is low and a more detailed study is required. Rejection of a plant is fatal for dealate queens since they can hardly find a new suitable host within 'walking distance'.

Does a foundress queen of *Cladomyrma petalae* select sympatric plants of the host spectrum other than their natal host under natural conditions? Indirect and circumstantial evidence comes from observations of climbing hosts in the field. Two liana species, *Strychnos vanprukii* and *Spatholobus bracteolatus* were found to climb sympatric host trees, *Saraca thaipingensis* and *Drypetes longifolia*, respectively. In each case (n=4), both the climber and the supporting tree harboured a single ant colony of *Cladomyrma petalae*, with the queen located either in the stem of the tree (n=3) or inside the climber (n=1). The workers of each colony had gnawed fresh nest chambers into young internodes of both partner species. This colonisation pattern suggests that the workers are capable of recognising host plants of the 'usual' host spectrum. [Note that non-host lianas climbing *Cladomyrma* host trees are, of course, never inhabited.]

Queens alighting on a host and checking internodes for their suitability as nest site presumably use several cues for host recognition (vision, olfaction and contact chemoreception). It is highly unlikely that the unrelated hosts show similarities in general stimuli such as whole scent profiles. In an ant/plant system involving species of a single genus only (*Macaranga*), odor profiles showed distinct interspecific variation (JÜRGENS et al. 2006). Even *Macaranga* species sharing the same obligate ant morphospecies (*Crematogaster* msp. 1, 2, 4) were found to show no obvious similarities in their scent profiles. The authors assume that ant queens may rely only on 'key stimuli', a few or a combination of several leaf compounds, for the choice of their specific host species.

In the case of the African tree *Leonardoxa africana*, ants of *Petalomyrmex phylax* workers are attracted by 'green-leaf volatiles' and methyl salicylate, which is emitted in high levels only by the young leaves (BROUAT et al. 2000). These compounds are reported as common components of numerous plant species belonging to a variety of plant families, and they are usually released from plants after herbivore attack (HEIL 2008). BENSON (1985) suggested that ant-plant symbioses originated from ants tending coccoids on plants. The ants might originally have used wound induced plant volatiles to find hosts infested with coccoids, as do parasitoid wasps and predaceous insects (CORTESERO, STAPEL & LEWIS 2000). Over evolutionary time, as a facultative ant-plant mutualism evolved into an obligate one, it has been hypothesised that ant-plants evolved to release ant-attracting volatiles even in the absence of herbivory, thus insuring worker patrolling of vulnerable plant parts and the encounter of host plants and foundress queens (BROUAT et al. 2000, EDWARDS et al. 2006).

While the precise nature of plant-derived signals are not yet clear, exaptations –pre-existing traits that acquired new functions– could also explain host plant recognition in the *Cladomyrma* system. Host plants of diverse phylogenetic affiliations may possess common substances related to herbivory (e.g., green-leaf volatiles and methyl salicylate). Driven by evolutionary interaction with their mutualistic ants, *Cladomyrma* host plants might have specialised in producing high concentrations of such compounds from intact young plant tissue, thus mimicing signals emitted by wounded leaves. Attraction of ant workers to damaged leaves has been demonstrated in a variety of ant/plant systems (e.g., FIALA & MASCHWITZ 1990, AGRAWAL & DUBIN-THALER 1999, LAPOLA, BRUNA & VASCONCELOS 2003, ROMERO & IZZO 2004, INUI & ITIOKA 2007).

In some cases, the compounds emanating from ant-plants have been found to be similar or identical to semiochemicals produced by the ants themselves. Some green-leaf volatiles, namely hexanal and 1-hexanol, of two myrmecophytic *Piper* species (MAYER, SCHABER & HADACEK 2008) are major components of the mandibular glands of major workers of *Oecophylla longinoda*. These chemicals cause an alarm and attraction response when presented to foraging workers (BRADSHAW, BAKER & HOWSE 1975). Another volatile organic compound of the two *Piper* ant-plants, the sesquiterpene β-caryophyllene, has been shown to evoke atagonistic behaviour in a leaf-cutting ant (NORTH, HOWSE & JACKSON 2000). Furthermore, methyl salicylate is similar to a compound produced by some ant species, methyl-6-methyl salicylate, which appears to be an alarm pheromone in some Ponerinae and a sex pheromone in *Camponotus* (DUFFIELD & BLUM 1975, HÖLLDOBLER & WILSON 1990).

The most accurate and reliable information, however, about host identity and suitability is usually gained via contact chemoreception (HEISSWOLF et al. 2007). On the plant surface, plant cuticular waxes can already give important information for host plant acceptance (MÜLLER & RIEDERER 2005). Typical behaviours before acceptance of a host are antennating, palpating, and test biting; behavioural patterns that are also observed in *Cladomyrma petalae* foundress queens during host assessment. To sum up, host recognition and acceptance by *Cladomyrma* might be achieved through qualitative or quantitative blends of host volatiles acting in concert with contact stimuli of the plant surface. This example shows the potential of the *Cladomyrma*/plant system as model for exploring the flow of information between mutualistic partners and for investigating the mechanisms involved in the restriction of many plant-ants to one or only a few host(s).

6. Acquisition of scale insects

6.1. INTRODUCTION

In obligate ant-plant mutualisms, host plants provide principally two different types of food for their ant partners, (i) directly through the production of specialised food bodies (and rarely extrafloral nectar), and/or (ii) indirectly via scale insects (Hemiptera: Sternorrhyncha: Coccoidea) which are tended by the ants inside hollow plant structures. Most of the symbioses between ants and myrmecophytes involve coccoids, they thus represent *three-partner systems* (BUCKLEY 1987, DAVIDSON & MCKEY 1993a). These coccoids feed in plant phloem and, after partial digestion of the plant sap, emit droplets of excreta known as honeydew (WILLIAMS & WILLIAMS 1980, DELABIE 2001). The honeydew is a complex mixture of sugars and other nutrients such as amino acids (MITTLER 1957, AUCLAIR 1963, WAY 1963, SALEH & SALAMA 1971, WÄCKERS 2000, YAO & AKIMOTO 2001, BLÜTHGEN, GOTTSBERGER & FIEDLER 2004). Honeydew is often enriched relative to plant sap by the upgrading of non-essential to essential amino acids by bacterial symbionts of coccoids (review in DAVIDSON & PATRELL-KIM 1996). Although honeydew contains only low amounts of amino acids and other nitrogen sources (BECERRA & VENABLE 1989), it has been proposed that exudates of coccoids might play a vital part in the nutrition of many arboreal ant species (DAVIDSON et al. 2003, BLÜTHGEN, STORK & FIEDLER 2004).

The species of the Southeast Asian plant-ant genus *Cladomyrma* appear to essentially depend on honeydew eliminated by their associated trophobiotic coccoids. Neither during field observations nor in staged encounters with herbivorous insect larvae placed onto young leaves, *Cladomyrma* ants were ever observed to feed on the insects they killed (see page 244), rather the ants simply chased them off or discarded them from the leaves.

Several other factors also support the hypothesis that honeydew is sufficient to supply a (nearly) complete diet for *Cladomyrma* ants: (i) populations of coccoids are maintained in hollow plant internodes throughout the life of a colony; (ii) *Cladomyrma* workers do not forage regularly off their host; (iii) plant-derived food sources such as extrafloral nectar (EFN) or food bodies are not provided by host plants of *Cladomyrma* (p. 219), except in *Saraca thaipingensis* where foliar nectaries are active on young developing leaves. However, the ants were observed to exploit EFN of *Saraca* only under starving conditions (p. 219). This may also explain the observation of TANAKA et al. (2007) who found workers of *Cladomyrma andrei*, a resident of the liana

Spatholobus, on EFN of *Mallotus*; (iv) when disturbed workers carry trophobiotic mealybugs into safety; and (v) the ratio of the nitrogen isotopes $^{15}N/^{14}N$ obtained from two *Cladomyrma* species, *C. andrei* and *C. dianeae*, was among the lowest measured for a wide set of arboreal ant species and did not differ from those of sap-feeding insects (DAVIDSON et al. 2003). According to this study, strikingly low $\delta^{15}N$ ratios are typical for many plant-ants and indicate N sources other than predation or scavenging (because the lighter isotope is lost in catabolic reactions and leads to progressive enrichment of ^{15}N relative to ^{14}N with increasing trophic level).

Honeydew thus appears to be an essential source of colony nutrition in *Cladomyrma* ants. One question immediately arising from this fact is, how the coccoids enter newly founded nests and thus secure the successful establishment of the ant colony on the host plant. In obligate ant-plant mutualisms the partners are horizontally transmitted, i.e, descendants of both plant and ant disperse independently from each other and must associate anew in each generation. The third partner, the trophobionts, may also disperse on their own, e.g., are dispersed by wind (STEPHENS & AYLOR 1978, WASHBURN & WASHBURN 1984, HECKROTH et al. 1998).

Another possibility is that founding ant queens carry the coccoid symbionts in their mandibles during the nuptial flight and colony foundation, thus establishing a honeydew source for the newly founded nest (GULLAN 1997, WILLIAMS 1998). This mode of vertical transmission of trophobionts has been recorded for ant species of the genus *Acropyga* (BÜNZLI 1935, WEBER 1944, BROWN 1945, FLANDERS 1957, BUSCHINGER et al. 1987 (as '*Plagiolepis*' but now identified as *Acropyga nearctica*), WILLIAMS 1998, LAPOLLA, COVER & MUELLER 2002, LAPOLLA et al. 2008), for the bamboo-dwelling *Tetraponera binghami* (KLEIN et al. 1992), and once for an unidentified *Cladomyrma* species (ROEPKE 1930). According to REYNE (1965, p. 150), however, this *Cladomyrma* has been wrongly identified and is an *Acropyga* (*Atopodon*) species instead. *Acropyga* alates with mealybugs in their mandibles have been found preserved in Miocene Dominican amber, indicating that this behaviour has existed for at least 15-20 million years (JOHNSON et al. 2001).

Vertical transmission of ant and trophobiotic coccoid from one generation to the next may also be achieved by colony budding or phoresis. In the former, newly mated ant queens return to their maternal nest (or to other conspecific nests), and leave it with a part of the colony's workers which carry brood and trophobionts to the new nest site (DILL, WILLIAMS & MASCHWITZ 2002, KAUFMANN et al. 2003). In the latter, trophobionts *actively* mount and cling to the ant's body. [Note that the term phoresis is used here in a strict sense, excluding cases in which trophobionts are picked up by an ant.]

Several mealybug species of the tribe Allomyrmococcini have been described to ride on workers of Asian *Dolichoderus* 'herdsmen' ants in different functional contexts, e.g., after disturbance and during change of trophobiotic sites or nest relocation (WILLIAMS 1978, MASCHWITZ & HÄNEL 1985, DILL, WILLIAMS & MASCHWITZ 2002). Co-dispersal of trophobionts and ant foundresses via phoresis apparently is rare, it has only once been suggested for the African plant-ant *Aphomomyrmex afer* associated with the mealybug *Paraputo anomala* (GAUME, MATILE-FERRERO & MCKEY 2000). The evidence presented, however, is indirect and alternative explanations might apply as well (see below).

In many examples of obligate ant-plant mutualism (including those involving *Aphomomyrmex* and *Cladomyrma*) the foundress ant must at least cut an entrance hole to gain access into the (hollow or pithy) domatium of the host plant, thus foundresses need unencumbered mandibles to chew into plant tissue (MOOG 1991, GULLLAN, BUCKLEY & WARD 1993). This problem does not exist for foundresses of the only plant-ant, *Tetraponera binghami*, reported to carry mealybugs in their mandibles (KLEIN et al. 1992), because they enter the hollow bamboo internodes only through holes already opened by stem-boring insects. In soil-nesting *Acropyga*, the only other known case where ant queens carry coccoids in their mandibles during the nuptial flight, the access to founding chambers is gained through soil crevices, and tasks for which unencumbered mandibles are needed (nest enlargement and sealing of entrance pores) are performed by the foundress *after* the mealybugs have been attached to the roots (BÜNZLI 1935, p. 554).

Phoresis is a plausible mechanism to circumvent the handicap of mandible-transport with respect to nest construction by plant-ants and is thus certainly an interesting alternative to mandible-transport of trophobionts. In light of these considerations, phoretic transport of trophobionts by foundresses may occur more frequently in plant-ants than current literature suggests. In a previous study on two *Cladomyrma* species inhabiting the tree *Saraca thaipingensis* and *Crypteronia griffithii*, MASCHWITZ et al. (1991) hypothesised that coccoids are not carried by founding queens and they assumed that the trophobionts arrive at the host plant via wind dispersal. The authors also observed conspicuous tiny slits along the outside of the founding chamber in *Saraca* which are chewed by the founding female, presumably enabling mealybug crawlers to enter the nest.

The aim of this study is to clarify these preliminary results and to assess whether the (early) arrival of scale insects in founding chambers is an indispensable condition for the formation of a *Cladomyrma*-plant association. Specifically, the objectives are (i) to

determine when and how trophobionts are acquired and (ii) to assess the role of trophobionts for the successful establishment of *Cladomyrma* on its host.

6.2. MATERIAL AND METHODS

Study sites and species investigated

The study was primarily conducted in Peninsular Malaysia at the Ulu Gombak Field Station (3°19'N, 101°45'E, 250 m a.s.l.) and in the hill regions of the Gombak valley, (400-800 m a.s.l.). Additional data were obtained from Lambir Hills NP (4°20'N, 113°50'E, Sarawak) and Poring Hot Springs (6°02'N, 116°42'E, Sabah) in Borneo. Information about the sites and climate is provided in MEDWAY (1972) and DAVIS, HEYWOOD & HAMILTON (1995).

In the present study, data were obtained from seven established *Cladomyrma* species and a possible eighth: *C. andrei* (Emery), *C. aurochaetae* Agosti, Moog & Maschwitz, *C. crypteroniae* Agosti, Moog & Maschwitz, *C. dianeae* Agosti, Moog & Maschwitz, C. *hewitti* (Wheeler), *C. maschwitzi* Agosti, *C. petalae* Agosti, and probably *C. maryatiae* Agosti, Moog & Maschwitz. Host plants include the woody climbers *Callerya nieuwenhuisii* (J.J. Sm.) Schot and *Spatholobus oblongifolius* Merrill, and the trees *Crypteronia griffithii* Clarke in Hook. f., *Saraca thaipingensis* Cantley ex Prain, and several species of *Neonauclea* Merrill.

The trophobionts collected from *Cladomyrma* nests (Fig. 6-6B-D) belong to a wide range of taxa, mainly Pseudococcidae (WILLIAMS 2004). They include *Crenicoccus cladomyrmae* Williams, *C. gullanae* Williams, *Crisicoccus theobromae* Williams & Watson, *Exallomochlus hispidus* (Morrison), *Hordeolicoccus crypteroniae* Williams, *H. heterotrichus* Williams *H. nephelii* (Takahashi), *Maconellicoccus multipori* (Takahashi), *Paracoccus interceptus* Lit, *Paraputo areolatus* Williams, *P. capillulatus* Williams, *P. cubicus* Williams, *P. danzigae* Williams, *P. domatium* Williams, *P. drypetis* Williams, *P. latebrae* Williams, *P. limitaneus* Williams, *P. lisponotus* Williams, *P. malesicus* Williams, *P. odontomachi* (Takahashi), *P. ranauensis* Williams, *P. sekayuensis* Williams, *P. spatholobi* Williams, *P. specicola* Williams, *Planococcus angkorensis* (Takahashi), *P. lilacinus* (Cockerell), *P. minor* (Maskell), *Pseudococcus aurantiacus* Williams, and *P. cryptus* Hempel. The dominant associates of *Cladomyrma* appear to be species of several *Paraputo* groups. Some of the pseudococcids associated with *Cladomyrma* ants, e.g., *Exallomochlus hispidus*, *Maconellicoccus multipori*, and *Pseudococcus cryptus*, are remarkable for their extreme broad host range (WILLIAMS 1996, BEN-DOV, MILLER & GIBSON 2009).

Coccidae are rare in most *Cladomyrma*-plant associations. Established colonies of *Cladomyrma* usually tend pseudococcids as the sole trophobiont but occasionally coccids occur within the same colony. In contrast, colonies of *Cladomyrma maschwitzi* often utilise a higher proportion of coccids relative to pseudococcids. Coccids as sole trophobionts have been found rarely in Cladomyrma nests, i.e., in *Cladomyrma crypteroniae* (n=1), *C. maschwitzi* (n=4), *C. nudidorsalis* (n=1), and *C. petalae* (in *Ryparosa*: n=1, in *Strychnos*: n=1). The taxonomic identity of the coccids is unknown in most cases. Identifications of a small sample by P. GULLAN and H.-P. HECKROTH revealed that several *"Coccus"* species are involved, e.g., *C. macarangae* Morrison and *C. secretus* Morrison. These two species regularly occur within the hollow internodes of several *Macaranga* ant-plants inhabited by *Crematogaster* ants (HECKROTH et al. 1998). However, the *Coccus* species described from *Macaranga* hosts are not congeneric with the type species of *Coccus* (L.) and a revision of these taxa is in progress (P. J. GULLAN and T. KONDO, pers. comm.).

Dispersal flight

Host plants producing young internodes were regularly checked in the field to directly witness whether or not alate females of *Cladomyrma* carry their trophobionts during the dispersal flight (Fig. 6-1A). Although founding queens were encountered mostly in the process of creating a founding chamber I was able to check a number of host-searching alates (n=13) for the presence of trophobionts. Dealate founding queens checking an internode for its suitability or chewing an entrance hole were also closely examined for any mandible-transported or phoretic trophobiont (n>50).

Colony founding

Colony founding in all *Cladomyrma* species is claustral. Foundresses of *Cladomyrma* chew their entrance holes into young internodes (Fig. 6-1B-D). After creating a founding chamber by removing the pith, the entrance hole is fully (or partially) blocked by debris (Fig. 6-1E). The margins of the holes soon develop wound calluses and begin to narrow the entrance. As a result, entrance holes become too narrow to permit the passage of a foundress. Most *Cladomyrma* species, except *C. maschwitzi* and *C. crypteroniae*, produce additional tiny slits (0.5–1.0 mm long, on average 0.7 mm) from within the founding chamber (Fig. 6-1E, Fig. 6-6A). These slits are termed '*secondary slits*' to distinguish them from the '*primary hole*' through which the foundress gained access into the internode. These 'secondary slits' are never created by workers when enlarging their nest into young plant parts, hence they are an excellent character signifying founding chambers on host plants.

I dissected internodes containing founding chambers to determine when trophobionts are acquired relative to the presence of brood or the first cohort of workers (nanitics). For each such internode encountered, I recorded whether the founding chamber contained a foundress, brood, trophobionts, or workers. I also examined the number of secondary slits and status of the primary hole (open, partially closed, and closed by pith debris or callus growth). Data were obtained from 7 *Cladomyrma* species.

For a subset of these data I estimated the exposure of the founding chambers to different light levels and grouped them into the categories 'shady' or 'sunny'. This allows a rough estimate of whether the number of secondary slits created by a founding female may be influenced by microclimatic conditions within the founding chamber. Since secondary slits are produced over a period of several days immediately after excavation of the initial nest chamber, I included in the analysis only those chambers in which brood had been found. The foundress produces her first brood usually *after* the chamber is fully excavated and the secondary slits are chewed, thus the presence of brood indicates that the final number of secondary slits is used for the analysis.

Experimental exclusion of trophobionts

To assess (i) when trophobiotic coccoids arrive at newly founded nests and (ii) whether arrival of these scale insects in founding chambers is an indispensable condition for the successful rearing of the first offspring, I first located in the field colony-founding queens of *Cladomyrma petalae* which were in the process of chewing an entrance hole into internodes of *Saraca thaipingensis*. The foundresses were carefully checked for any accompanying trophobiont without disturbing them in their task. [The foundresses become so absorbed in the excavation process that they can be examined from a distance of a few centimetres.] Once the founding queens entered the hollowed-out internode, a barrier of sticky resin (Tangle-trap, Tanglefoot Corp., Grand Rapids, Mich., USA) was applied around the internode in half of the new foundings (n=11), thus preventing coccoids from entering the nest chamber. The other foundings served as controls (n=11). After 19 to 108 days the nest chambers were collected. [Since detection of a foundress in the process of founding is a rare event, collection time was, unfortunately, mostly not determined by an optimal test design but by my departure from the study site.] As each internode was dissected, I recorded foundress survival (dead or alive), number of eggs, larvae, pupae, workers and/or coccoids, as well as number of secondary slits and length of founding chamber. In addition, I monitored four unmanipulated foundings of *C. petalae* after 1, 3, 6, and 8 days to better observe the arrival time of trophobionts in the founding chambers.

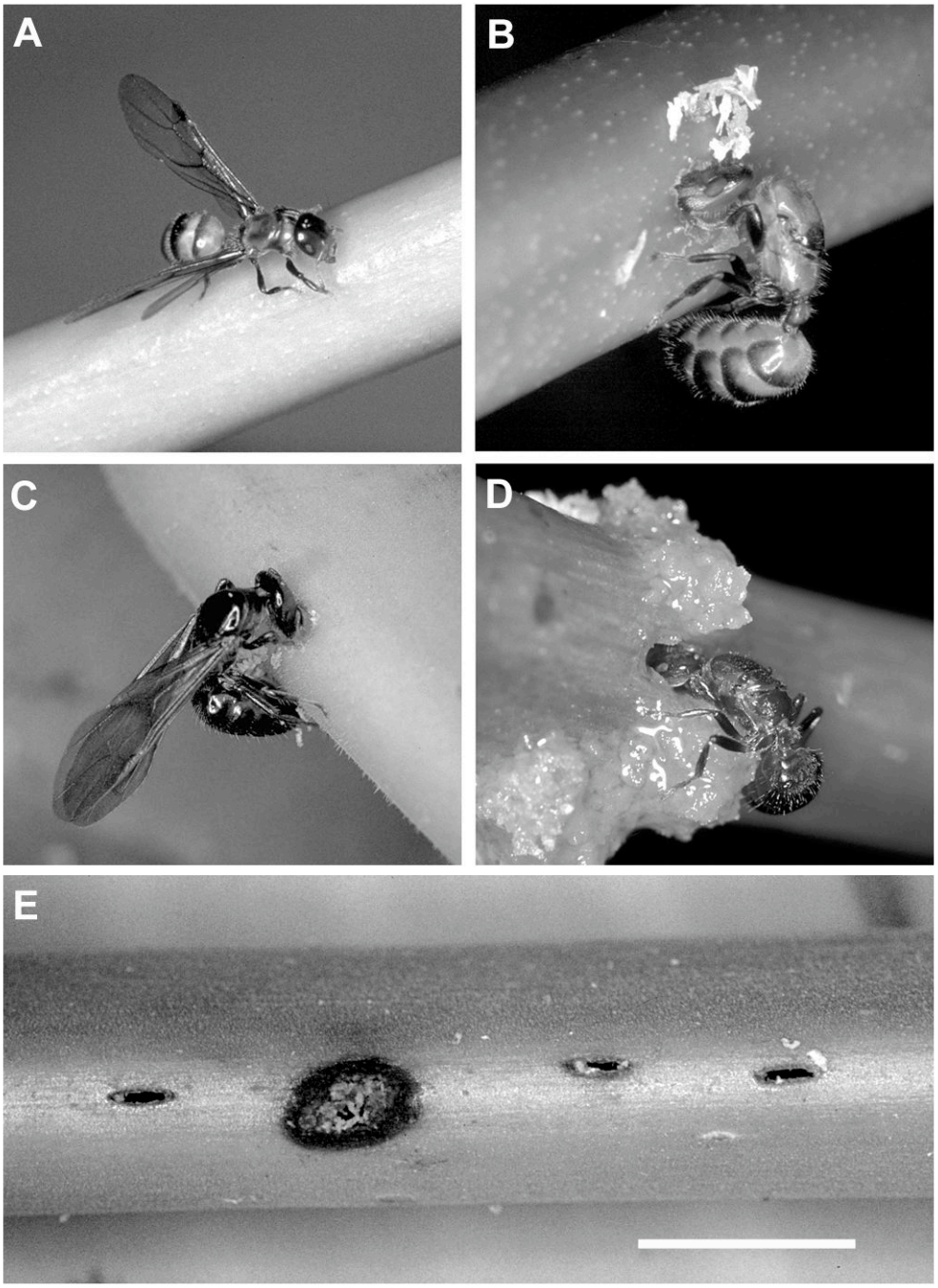


Figure 6-1: Colony-founding in *Cladomyrma* spp. **A**: alate *C. petalae* queen checking an internode of *Saraca thaipingensis* for its suitability as founding site. **B**: *C. petalae* chewing into an internode of *Saraca thaipingensis*. **C**: alate *C. dianeae* – *Neonauclea gigantea*. Most founding queens shed their wings prior to chewing an entrance hole. **D**: *C. maschwitzi* – *Crypteronia griffithii*. The hollowed-out pith of young internodes may be very moist. **E**: lateral side of domatium of *Neonauclea gigantea* showing 'primary hole' plugged with pith debris and three 'secondary slits'. Scale bar (for E only): 5 mm.

Active entry of immature mealybugs into founding chambers

In the family Pseudococcidae, there are four instars in the female. The three nymphal instars of most female pseudococcids are relatively mobile and the first-instar nymphs (called 'crawlers') are usually the main dispersal agents (GULLAN & KOSZTARAB 1997). To test whether pseudococcid nymphs are capable of entering founding chambers on their own, they were placed onto young twigs containing a founding chamber of *Cladomyrma*. First, I dissected a young *Saraca* twig occupied by a *Cladomyrma* colony, then removed the ants and waited until the coccoid nymphs, disturbed by their exposure, started to walk around. The nymphs (first and second instars) were carefully lifted with a wetted needle and placed onto an intact, unmanipulated twig at a distance of 3 centimetres from a founding chamber with open secondary slits (Fig. 6-5). The twig was fixed in a horizontal position to reduce a possible geotactic response of the immature mealybugs. However, I placed the nymphs onto the twig with their heads pointing into the direction of the founding chamber in case they walked in the opposite direction. A total of ten nymphs ranging in length from 0.5 to 1.5 mm were tested. Behaviour of each nymph was recorded for a 5-min period.

Primary hole

In contrast to other *Cladomyrma* species, *C. maschwitzi* does not create secondary slits. Whereas the entrances or 'primary holes' of founding chambers occupied by *C. petalae* are first blocked by pith remains and then closed by subsequent callus growth, those of founding chambers inhabited by *C. maschwitzi* remain open as a slit-like orifice for several weeks after foundation although callus growth has begun. By measuring the diameter of the primary hole in founding chambers with and without foundresses during a 40-day period, I tested the hypothesis that *C. maschwitzi* foundresses chew callus tissue and keep the primary hole open, thus potentially allowing the passage of coccoid crawlers. First, I selected eight young founding chambers with no or little callus growth and removed the foundresses from four chambers, the other half served as controls (foundress maintained). Then, the apex and base of each internode containing a founding chamber was coated with a sticky resin in order to prevent the arrival of other colony-founding queens which may recolonise empty chambers or take over existing foundations.

6.3. RESULTS

6.3.1. Dispersal flight

Alate host-searching females of *Cladomyrma crypteroniae* (n=1), *C. dianeae* (n=1), *C. hobbyi* (n=1), *C. maschwitzi* (n=3), and *C. petalae* (n=7) were witnessed during their dispersal flight. They had just landed on a host plant to check the suitability of a young twig for nest founding. None of these queens carried a trophobiont in their mandibles nor did I detect any phoretic trophobiont on the ant's body. In addition, dealate founding queens of *C. crypteroniae* (n=2), *C. dianeae* (n=5), *C. hobbyi* (n=1), *C. maschwitzi* (n=6), and *C. petalae* (n~40) wandering along an internode or chewing an entrance hole likewise were free of accompanying trophobionts.

6.3.2. Colony founding

The dissection of 338 founding chambers of eight *Cladomyrma* species (*andrei*, *aurochaetae*, *crypteroniae*, *dianeae*, *hewitti*, (*maryatiae*), *maschwitzi*, *petalae*) showed that coccoid abundance strongly increased with founding age in all species (Fig. 6-2). For the pooled data, the majority of founding chambers lacking brood contained no trophobionts (81.7%, 85 of n=104) whereas founding chambers with nanitic workers (minims) usually contained coccoids (93.6%, 44 of n=47). In the three cases in which the natal colony lacked coccoids (1x in *C. crypteroniae* and 2x in *C. petalae*), worker and brood numbers were low (1–2 workers, 0-7 eggs, 0–4 larvae, 0 pupae), probably indicating that resources were in short supply.

Arrival of trophobionts prior to the production of brood is not uncommon. About 18% of the foundations without brood already harboured coccoids. In *Cladomyrma petalae*, chewing of both the founding chamber and the secondary slits is completed within 5 to 6 days at the latest and egg-laying follows completion of the nest (MOOG 1991). It appears from these data that arrival of trophobionts can occur within the first few days after foundation, although absence of brood does not necessarily indicate recent founding (egg-laying may be delayed under unfavourable conditions or trophic eggs are consumed by the foundress). Coccids generally arrive later in *Cladomyrma* colonies than pseudococcids. The founding chambers examined usually did not contain coccids, except for *C. maschwitzi* where coccids were present in a few founding chambers (7.3%, 5 of n=68). This 'late arrival' of coccids may also reflect a selection process by the ant foundress which might prefer pseudococcids to coccids during the founding stage. Even incipient colonies beyond the stage of foundation have usually been found with pseudococcids and not with coccids.

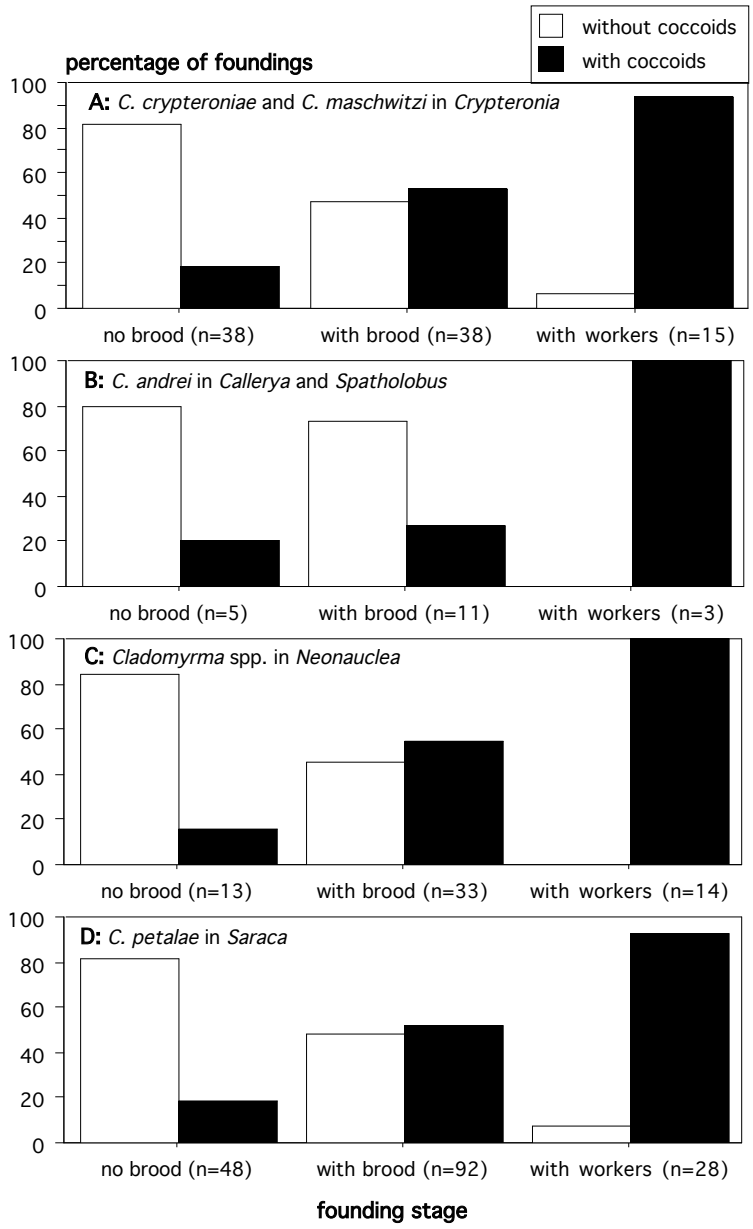


Figure 6-2: Distribution of coccoids in colony-founding chambers of *Cladomyrma* spp. grouped by founding stage. *No brood* = neither brood nor workers present. *With brood* = eggs, larvae or pupae, but no workers. *With workers* = first cohort of workers and (usually) brood, initial founding chamber excavated by the foundress not yet enlarged by workers. **C**: Species include *C. aurochaetae*, *C. dianeae*, *C. hewitti*, and probably *C. maryatiae*.

The secondary slits may serve two major, not mutually exclusive roles during the stage of foundation. They may either enhance microclimatic conditions within the founding chamber and/or facilitate the acquisition of trophobionts. A comparison of the number of secondary slits produced by the foundress ants between 'sunny' or

'shady' habitats yielded no significant effect of light on the number of secondary slits, neither in *Cladomyrma* species inhabiting *Neonauclea* nor in the *C. petalae-Saraca* association: Mann-Whitney U-test: $P = 0.072$, $n_{shade} = 7$, $n_{sun} = 31$, and $P = 0.097$, $n_{shade} = 28$, $n_{sun} = 63$, respectively (Fig.6-3; medium light levels were omitted from the analysis). However, the trend observed differed between the two associations. Whereas in the *Neonauclea* group the number of secondary slits was lower in shady habitats (but sample size for 'shade' was low), the trend followed the opposite direction in the *C. petalae-Saraca* group. A detailed experimental study is needed to test the influence of secondary slits on temperature and humidity within the founding chamber.

If the number of secondary slits positively affects the arrival of coccoids in founding chambers of *Cladomyrma* it is to be expected that founding chambers lacking coccoids are characterised by having fewer secondary slits than those containing coccoids. This analysis requires (i) that only foundations which contain brood are considered because the presence of brood indicates that the final number of secondary slits has been produced by the foundress ant, and (ii) that foundations 'with' and those 'without' coccoids are equally distributed between 'sunny' and 'shady' habitats. Using Fisher's exact test, this assumption is met: $P_{Neonauclea} = 0.66$, chi square 0.505, $df = 1$, and $P_{Saraca} = 0.65$, chi square 0.275, $df = 1$.

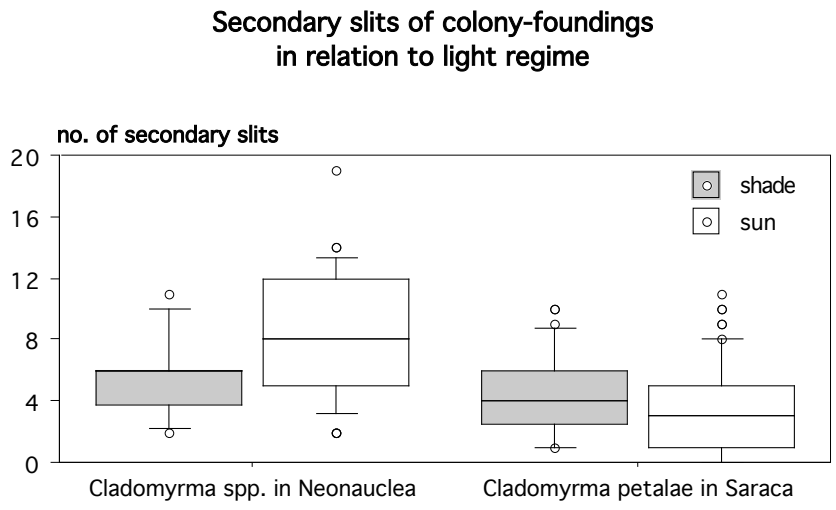


Figure 6-3: Number of secondary slits produced by *Cladomyrma* founding queens in relation to light regime (sunny or shady habitat). Ambiguous cases (medium light levels) have been omitted. Considered are only foundations which contained brood because the presence of brood indicates that no more secondary slits will be produced by the foundress. *Cladomyrma* spp. in *Neonauclea* (includes *C. aurochaetae*, *C. dianeae*, *C. hewitti*, and probably *C. maryatiae*): $n_{shade} = 7$, $n_{sun} = 31$; Mann-Whitney U-test, $P = 0.072$ (n.s.). *Cladomyrma petalae* in *Saraca*: $n_{shade} = 28$, $n_{sun} = 63$; U-test: $P = 0.097$ (n.s.).

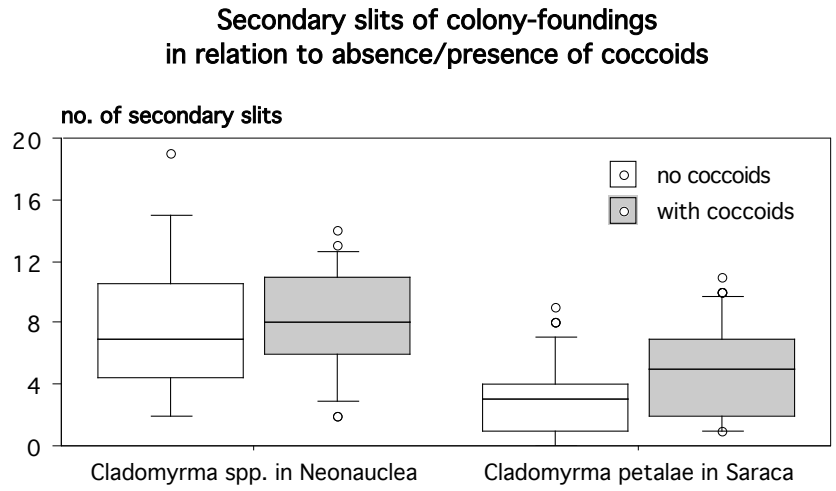


Figure 6-4: Number of secondary slits produced by *Cladomyrma* founding queens in relation to absence/presence of coccoids. Considered are only foundations which contained brood because the presence of brood indicates that no more secondary slits will be produced by the foundress. *Cladomyrma* spp. in *Neonauclea* (includes *C. aurochaetae*, *C. dianeae*, *C. hewitti*, and probably *C. maryatiae*): $n_{no\ coccoids} = 13$, $n_{with\ coccoids} = 18$; Mann-Whitney U-test, $P = 0.59$ (n.s.). *Cladomyrma petalae* in *Saraca*: $n_{no\ coccoids} = 44$, $n_{with\ coccoids} = 48$; U-test: $P = 0.018$.

The findings presented in figure 6-4 show contrasting results. In the *Cladomyrma-Neonauclea* association, the founding chambers lacking coccoids did not possess a significantly lower number of secondary slits than those having coccoids (Mann-Whitney U-test, $P = 0.59$, $n_{no\ coccoids} = 13$, $n_{with\ coccoids} = 18$). In the *C. petalae-Saraca* association, however, the number of secondary slits differed significantly between founding chambers with coccoids present or absent ($P = 0.018$, $n_{no\ coccoids} = 44$, $n_{with\ coccoids} = 48$).

Generally, *Cladomyrma* species colonising *Neonauclea* produced more secondary slits than *C. petalae*: mean = 8.1 ± 4.12 SD, median 7, n=33, versus mean = 4.0 ± 2.91 SD, median 4, n=92, respectively (only foundations 'with brood' considered). Even fewer secondary slits were chewed by *C. andrei* (mean 1.6 ± 1.37 SD, median 1, n=11). The secondary slits observed in *Cladomyrma-Neonauclea* foundations are always located on both lateral sides of the swollen internodes (domatia) at so-called 'prostomata', i.e., preformed, thin zones of the domatium where ants preferably chew their entrance holes. The prostoma has the form of a straight line running the entire length of the internode. It is highly plausible that foundresses producing secondary slits in prostomata invest less energy than those chewing into comparatively thick internode walls (as in *Saraca*). In addition, myrmecophytic *Neonauclea* are light-demanding species growing predominantly in open disturbed habitats. These two

factors, the easy creation of slits and the exposure to high light levels (temperature), may both affect the average number of secondary slits produced by *Cladomyrma* species colonising *Neonauclea* plants.

6.3.3. Experimental exclusion of trophobionts

Earlier I demonstrated that the number of coccoids inside nest chambers increases during the founding stage and that all foundations containing workers usually also contain coccoids (Fig. 6-2).

Table 6-1: Developmental stage of colony foundings of *Cladomyrma petalae* in *Saraca* collected after 19 to 108 days. Experimental group (coccoid access to founding chambers prevented by sticky resin applied around twigs): n = 11. Control group (unmanipulated foundings): n = 11. Mann-Whitney U-test: $P_{pseudococcids} = 0.0003$, $P_{workers} = 0.006$, $P_{eggs} = 0.0003$, $P_{larvae} = 0.23$, $P_{pupae} = 0.006$.

Experimental group

days after founding	queens († = dead)	no. pseudococcids	no. workers	brood : eggs + larvae + pupae
19	1	0	0	0 + 3 + 0
19	1	0	0	8 + 0 + 0
29	1	0	0	2 + 1 + 0
36	1	0	0	4 + 4 + 0
36	1	0	0	0 + 3 + 0
52	1	0	0	0 + 3 + 0
53	1	0	0	0 + 1 + 0
75	1†	0	0	0 + 0 + 0
75	1†	0	0	0 + 0 + 0
75	1†	0	0	0 + 0 + 0
91	1†	0	0	0 + 0 + 0

Control group

days after founding	queens	no. pseudococcids	no. workers	brood : eggs + larvae + pupae
19	1	1	0	3 + 0 + 0
21	1	1	0	14 + 0 + 0
22	1	0	0	2 + 0 + 0
48	1	3	3	32 + 4 + 2
49	1	0	0	6 + 0 + 0
50	1	6	4	54 + 7 + 1
51	1	5	3	18 + 11 + 3
62	1	4	7	35 + 8 + 6
65	1	3	0	50 + 0 + 0
72	1	2	3	7 + 13 + 1
108	1	4	6	24 + 15 + 8

Are the trophobionts essential during the founding stage of *Cladomyrma* to successfully produce the first cohort of workers? The experimental founding chambers (coccoids excluded) of *Cladomyrma petalae* dissected after 19 to 36 days all contained eggs and/or larvae, thus this subset of the experimental group appeared to be equally successful in producing brood as did the subset of the control group dissected between the 19th and 48th day (Tab. 6-1). In the control group the first cohort of workers was found after 48 days, and only two of eight foundresses checked after the 6th week had failed to produce workers. In contrast, none of the experimental foundations dissected after the 6th week contained workers.

Except for the number of larvae the two groups differed significantly in the number of pseudococcids, eggs, pupae and workers: $P_{pseudococcids}$ = 0.0003, $P_{workers}$ = 0.006, P_{eggs} = 0.0003, P_{larvae} = 0.23, P_{pupae} = 0.006 (Mann-Whitney U-test). However, the two groups did not differ in the number of secondary slits (P = 0.66), chamber length (P = 0.37) or collection time (P = 0.82), indicating that differences are due to the absence/presence of coccoids.

Strikingly, all four foundresses of the experimental group collected after the 10th week were found dead and mouldy (Tab. 6-1). Dates of death could not be determined. Small chamber length and low number of secondary slits usually indicate early death of a foundress shortly after founding, however, the two parameters were obviously not very different from those of the control group (*secondary slits*: $mean_{dead}$ 3.0 ± 1.41 SD versus $mean_{control}$ 4.4 ± 2.81 SD; *chamber length*: $mean_{dead}$ 2.85 cm ± 0.35 SD versus $mean_{control}$ 3.4 cm ± 0.63 SD). The founding chambers containing the dead foundresses were intact but the primary holes and the secondary slits were fully closed by callus tissue. Combined with the degree of decomposition of the ants I assume that death had occurred at least 1 or 2 weeks prior to collection. This narrows the date of death to a period between the 2nd and 8th or 9th week after founding. Although the available evidence is suggestive of contributing foundress death to the absence of coccoids, it cannot be ruled out that deaths are due to unknown causes and that all occurred in the experimental and not the control groupby chance.

The census of four additional, unmanipulated colony foundings of *Cladomyrma petalae* after 1, 3, 6 and 8 days revealed that pseudococcids may arrive as early as the first day after foundation. All four foundresses were observed during their founding process and were not accompanied by mealybugs. However, I found a mealybug crawler in each of the founding chambers collected after one and three days. The two remaining nest chambers were free of trophobionts. In most cases the primary hole was fully plugged by the foundress with pith debris, except in the founding dissected

after 1 day. Here, the pith plug left a slit big enough for the passage of a mealybug crawler. This founding still lacked secondary slits but they were present in the other three foundations. This observation illustrates that even a single tiny slit may be detected and entered by a crawler shortly after colony founding.

6.3.4. Active entry of immature mealybugs into founding chambers

Pseudococcids are almost exclusively the first arrivals in *Cladomyrma*-founding chambers (see above, Fig. 6-6B). I therefore tested the capability of immature pseudococcids to enter founding chambers on their own. Because species of Pseudococcidae could not be identified in the field, they were pooled and are referred to as ‘pseudococcids' or 'mealybugs' in the following analysis.

Immature mealybugs were placed onto a young *Saraca* internode inhabited by a foundress of *Cladomyrma petalae* (Fig. 6-5). The results show that active entry of pseudococcids into founding chambers is a regular phenomenon under the conditions chosen for the experiment (Tab. 6-2).

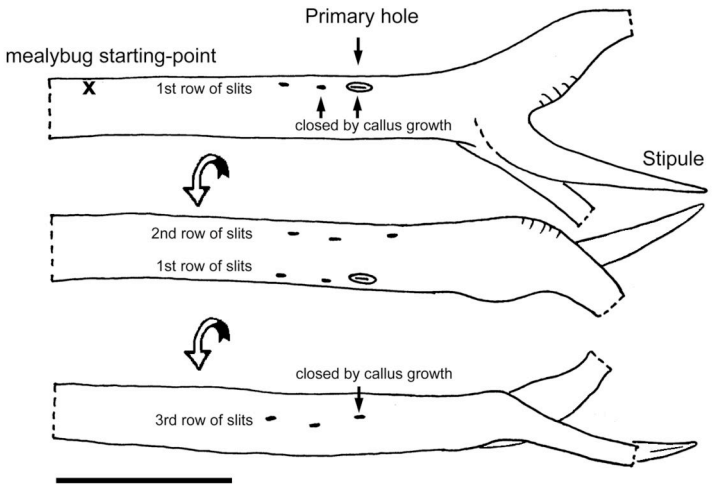


Figure 6-5: Distribution of three rows of secondary slits around a *Saraca* internode (rotated by about 90° and 180°, respectively). A founding queen of *Cladomyrma petalae* had produced from inside her founding chamber a total of eight secondary slits. The 'primary hole' (through which the foundress gained access) and two secondary slits were closed by callus growth. X indicates the starting-point of the mealybug experiment. Scale bar: 3 cm.

Table 6-2: Behavioural tests with immature pseudococcids (first and second instars) placed onto a *Saraca* internode close to a founding chamber of *Cladomyrma petalae* (see Fig. 6-5). Head of mealybug pointing towards foundation at start of the experiment.

fate of mealybug	mealybug size [mm]	time [sec]	notes
falls down:	1.0	43	changes direction, moves some cm, falls down by unknown cause
settles in depression:	0.8	68	passes 3 slits closely, settles in pit of closed slit (3rd row)
	0.6	135	changes direction, 'circles' around twig, resting in leaf axil
hides under plant structure:	1.5	94	passes several slits (by 1mm), hides under stipule
	0.9	250	changes direction twice, finally hides under leaf base
enters secondary slit:	0.7	57	moves in curves, reaches 2nd row of slits, enters 2nd slit
	1.2	59	moves in a curve, reaches 1st row of slits, enters 1st slit
	0.5	63	closely passes slit, enters 2nd slit of 3rd row
	0.6	77	moves in a curve, enters 1st slit of 2nd row
	0.7	78	passes 2 slits closely, reaches 3rd row of slits, enters 2nd slit

Of the ten mealybugs tested, five successfully located and entered the foundations (Tab. 6-2). On average, the mealybugs needed 66.8 seconds (± 10.010 SD; n=5) to cover the distance from their starting-point to the foundation and to disappear into the slits produced by the ant foundress. On reaching a slit the pseudococcids all appeared to enter it without hesitation. However, the pseudococcids were often observed to narrowly pass slits (ca. 1 mm), apparently without recognising their proximity. Of the five remaining mealybugs tested, two settled in depressions on the external surface of the plant (closed secondary slit, leaf axil) and two hid under plant structures (stipule, leaf base). Thus, 'hiding' was the predominant behavioural response of immature mealybugs within the 5-min observation period. Only a single mealybug failed to find a hiding place and fell to the ground due to an unknown cause.

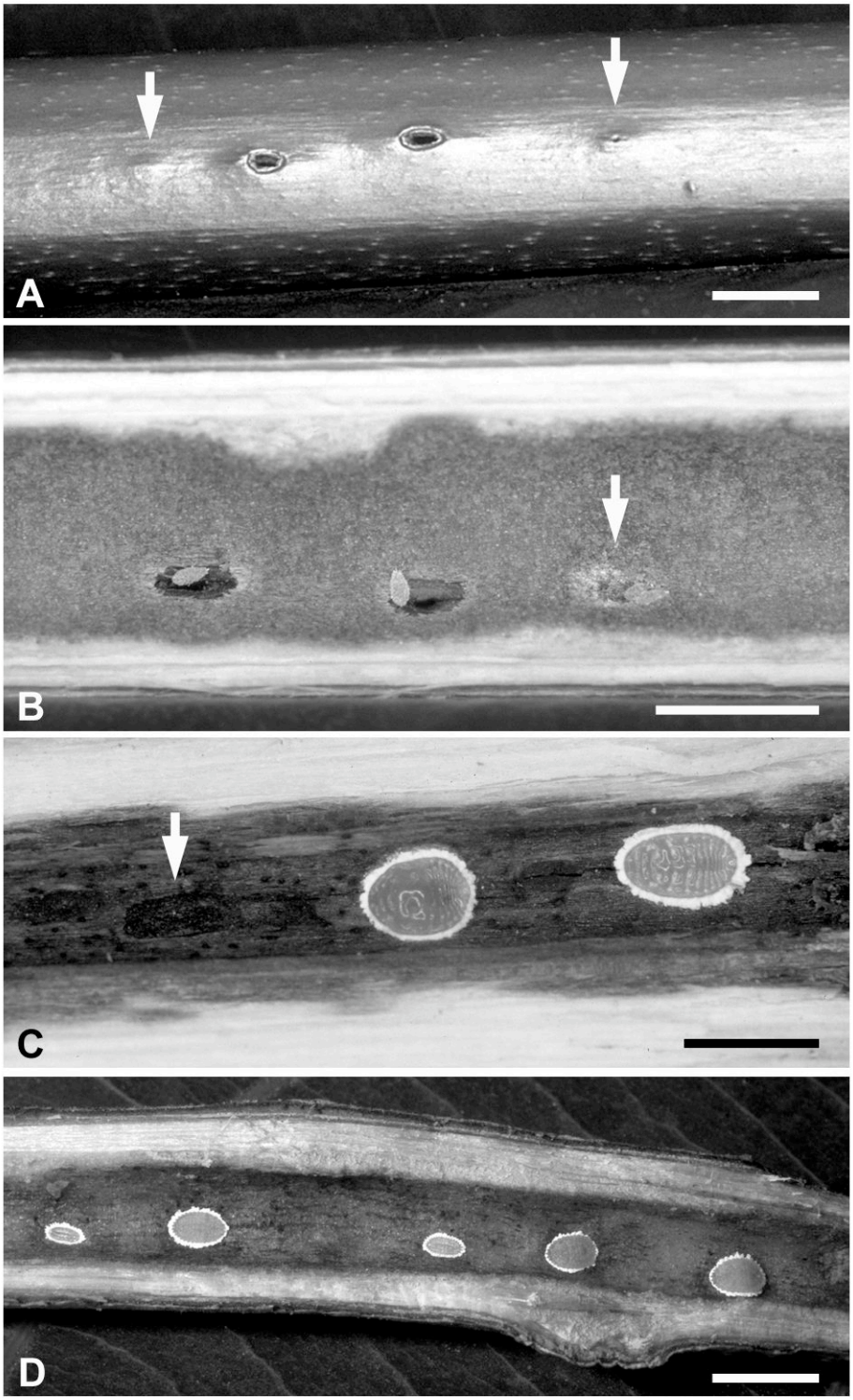


Figure 6-6: Secondary slits and pseudococcids in dissected nest chambers of *Cladomyrma* spp. **A**: secondary slits produced by a *C. petalae* foundress. Note the unfinished slits visible as small elevations on the external surface (arrows). They correspond to small depressions in the interior of the nest chamber. **B**: mealybug crawlers inside a founding chamber of *C. petalae*. They entered the nest through the secondary slits and settled in depressions gnawed by the foundress (arrow). **C**: mealybugs (near *Paraputo*) inside a mature *Saraca* twig. Arrow indicates a feeding site (mealybug removed). **D**: row of mealybugs (near *Paraputo*) in *Drypetes longifolia*. Scale bar: 3 mm.

6.3.5. Primary hole

Secondary slits are not produced by founding queens of *Cladomyrma maschwitzi* inhabiting the tree *Crypteronia griffithii*. Nevertheless, the abundance of coccoids inside their founding chambers increases with founding stage much in the same way as in *Cladomyrma* species producing secondary slits (Fig. 6-2A). How do the coccoids find their way into the foundations? I observed that the entrance (primary) holes of *C. maschwitzi* remained open as slit-like orifices for several weeks after foundation although callus growth had begun. Is the foundress responsible for maintaining an orifice by chewing the wound callus? The effect of foundress exclusion on primary hole diameter relative to that of the controls (foundresses maintained) is presented in figure 6-7. After about 4 to 5 weeks the primary hole was fully closed by callus tissue in the experimental group (n=4). In contrast, the diameter of the primary holes of inhabited founding chambers (n=4) decreased more slowly and then remained more or less constant during the last week of the 40-day study period.

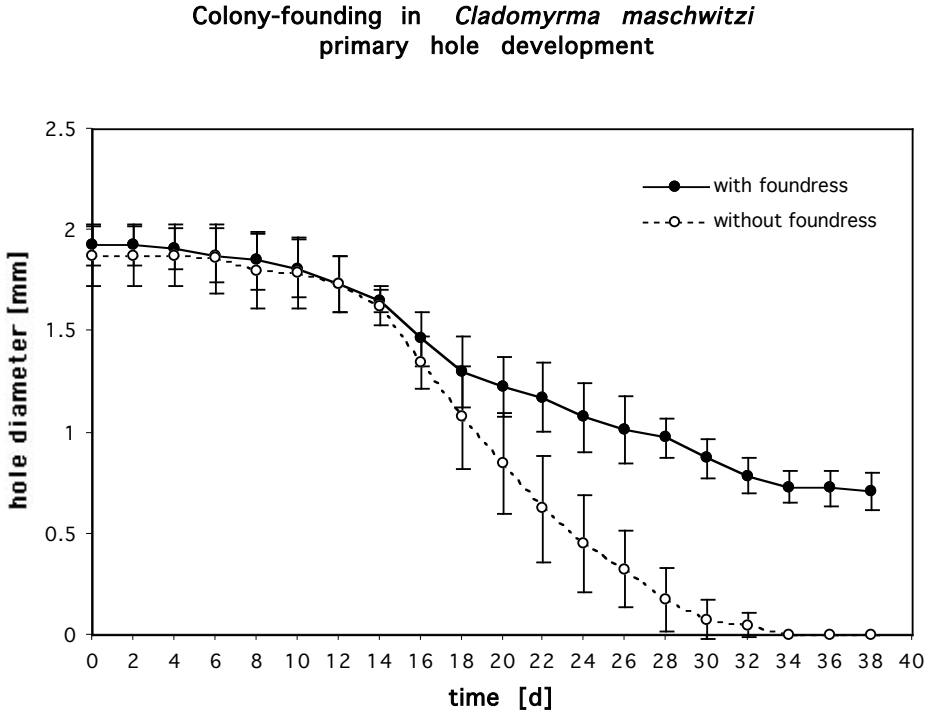


Figure 6-7: Time course of entrance (primary) hole size during colony-founding by *Cladomyrma maschwitzi* inhabiting the tree *Crypteronia griffithii* over a 40-day period. The diameter given refers to the hole margins and excludes pith debris that may plug the hole. Experimental group (foundress excluded): n = 4. Control group (foundress maintained): n = 4. Error bars = ± 1 SD.

It is interesting to note that foundresses of *C. maschwitzi*, prior to callus growth, plug the primary hole during the first days after founding with pith debris as do other *Cladomyrma* species. The nest entrances are, however, rarely fully plugged; the foundresses usually maintain an orifice by incompletely blocking the primary hole. As a rule, secondary slit-producing *Cladomyrma* foundresses completely plug the primary hole and allow them to grow over whereas those of *C. maschwitzi* maintain an orifice at the primary hole throughout the founding stages.

6.3.6. Summary of the results: acquisition of scale insects

- trophobiotic coccoids are not carried by founding queens of *Cladomyrma* during their dispersal flight
- the number of coccoids in founding chambers increases with foundation age, and during the stage of first worker emergence coccoids are virtually always present
- small 'secondary slits' produced by *C. petalae* foundresses facilitate access of coccoids (additional functions of the slits, e.g., enhancing microclimatic conditions, are not excluded)
- pseudococcids are the first arrivals in founding chambers of *Cladomyrma*, even in *Cladomyrma* species which tend mixed pseudococcid-coccid populations later in their colony development
- exclusion experiments suggest that in the absence of pseudococcids the foundresses of *C. petalae* are not capable of successfully rearing the first cohort of workers
- a behavioural test shows that after dispersal immature mealybugs have the tendency to hide and they readily enter slits
- *C. maschwitzi* foundresses produce no secondary slits but keep an orifice in the primary hole open during the foundation stage

6.4. DISCUSSION

6.4.1. Co-dispersal

One main result emerging from this study is that *Cladomyrma*-founding queens do not carry trophobiotic coccoids during their dispersal flight. In total, I examined 13 alate host-searching queens and more than 50 dealate queens in the process of nest excavation for the presence of coccoids. The *Cladomyrma* foundresses neither carried coccoids in their mandibles nor were coccoids carried phoretically on the ants' bodies. Thus the previous hypothesis of MASCHWITZ et al. (1991) that coccoids arrive independently of the ants on the host plant is confirmed by this study. Nevertheless, vertical transmission via co-dispersal of ant foundresses and coccoid trophobionts has been suggested to occur more frequently in plant-ants than currently reported (GAUME, MATILE-FERRERO & MCKEY 2000). In the following, I briefly review the existing evidence for coccoid transport in plant-ants and conclude that there is little evidence to assume a more widespread occurrence of the co-dispersal phenomenon.

In plant-ants, two modes of vertical transmission of ant and coccoid are known: coccoid-carrying in the mandibles during the nuptial flight (KLEIN et al. 1992, WILLIAMS 1998, LAPOLLA 2004) and phoresis (GAUME, MATILE-FERRERO & MCKEY 2000). The third known mode, transport by ant workers during colony budding (DILL, WILLIAMS & MASCHWITZ 2002), is no option for host-specific plant-ant foundresses whose host plants are scattered as isolated resources ('islands') in the forest.

The behaviour of coccoid-carrying during the nuptial flight by ant queens is similar to that of Attine ants where queens disperse and mate carrying a mycelium piece of symbiotic fungus in the infrabuccal pocket (IHERING 1898). In general, however, swarming ant queens are rarely reported to improve founding success by carrying 'resources' (other than internal fat reserves) to a new nest site. An often cited example is *Carebara vidua*, an inquiline of termite mounds; the large, newly mated queens have some tiny workers clinging to the legs and body as they fly off and, after founding, the workers are presumed to assist in rearing the first offspring (ARNOLD 1915-1924, WHEELER 1936, HÖLLDOBLER & WILSON 1990). According to LEPAGE & DARLINGTON (1984), however, *Carebara* workers do not assist in colony founding. Although some workers were carried by departing queens, they presumably dropped off later, because the authors never found workers with dealate queens after they had dug themselves in. Furthermore, queens kept in the laboratory successfully reared young colonies without the help of accompanying workers.

SEIFERT & HELLER (1999) reported that a foundress of *Acropyga paleartica* carried a worker pupa during dispersal. However, this single observation possibly represents a mistake by the foundress ant which mistook a worker pupa for a mealybug (see also LAPOLLA 2004).

Likewise, coccoid-carrying by plant-specialist ants during the nuptial flight is not well understood. Although STOUT (1979) and SCHREMMER (1984) suspect mandible-transport of trophobiotic coccoids by plant-ant foundresses of *Myrmelachista* and *Pseudomyrmex*, respectively, it has only been confirmed once for *Tetraponera binghami* (KLEIN et al. 1992). What could explain the rarity of such behaviour in plant-ants? With the exception of *Tetraponera binghami* which gains access through holes already present in bamboo internodes, plant-ant foundresses usually have to actively force their entry into their host. A hypothesis put forward is that they thus need unencumbered mandibles to chew into plant tissue (MOOG 1991, GULLAN, BUCKLEY & WARD 1993). If coccoids are indeed carried in the mandibles the founding female must release the trophobiont for the whole period of entrance chewing and nest excavation (taking minutes to hours). It seems unlikely that the coccoid would stay during the whole excavation process at the place where it has been dropped.

One option to circumvent this difficulty would be to carry coccoids in an inactive condition. There is only a single report that such may be the case in the hypogaeic ant *Acropyga fuhrmanni*. FLANDERS (1957, p. 535) observed that each *Acropyga* foundress carries a coccoid and the author deduced that "since the queen in order to excavate her nest must lay aside the stem-mother coccid, the latter is supposedly in an inactive condition." According to BÜNZLI (1935), however, *Acropyga* queens gain access to their founding chamber through soil crevices, and coccoids are attached to the roots *prior* to tasks concerning nest enlargement or plugging of entrance pores.

A second option for plant-ants is that foundresses carry trophobionts phoretically, thus their mandibles can still be used for nest access and excavation. Again, the single report by GAUME, MATILE-FERRERO & MCKEY (2000) on the African plant-ant *Aphomomyrmex afer* nesting in domatia of the tree *Leonardoxa* is based only on indirect evidence. Of 19 *Aphomomyrmex* foundresses located in their claustral phase (with no workers or a few nanitic workers), 12 had at least a single pseudococcid in their founding chamber. One of the foundresses had two second-instar mealybugs attached to her body, and the remaining seven foundations contained no coccoids. According to GAUME, MATILE-FERRERO & MCKEY (2000) these results strongly suggest that mealybug and ant may co-disperse by phoresis of juvenile female mealybugs on

founding queens. Unfortunately, the authors witnessed no foundress in the process of entering a domatium.

GAUME, MATILE-FERRERO & MCKEY (loc. cit.) discuss at length alternative explanations of their observation but conclude that co-dispersal via phoresis is the most likely explanation. However, sample size in their study was low and, in my opinion, two factors may explain both the presence of mealybugs in founding chambers of *Aphomomyrmex* queens and the firm attachment of mealybugs to a foundress. First, it cannot be excluded that mealybugs entered the founding chambers on their own accord. This is supported by the fact that *Aphomomyrmex* foundresses only partially block the entrance hole (Gaume et al. 2000), leaving a narrow passage that could permit entry of first instar nymphs. Second, the authors argue (p. 89) that the two nymphal mealybugs "were firmly attached to the queen's body, since they were not removed by the alcohol in which the domatium's contents were killed and stored." However, instead of supporting their reasoning, the flooding of the domatium with alcohol to kill and preserve the inhabitants (prior to examining the domatium!) might actually be the *cause* for finding mealybugs attached to the foundress' body. It appears not unlikely that this catastrophic event caused a frantic response in both the ant and the mealybugs trying to escape their deadly prison, finally leading to their being clung to each other in their death throes. Yet, even if phoretic transport of coccoids by *Aphomomyrmex* ants during their dispersal flight is not unambiguously supported by this study, the authors deserve credit for drawing attention to a mostly neglected aspect of colony founding in ants.

Evidence that may support the assumption of phoretic transport of immature mealybugs by *Aphomomyrmex* foundresses comes from a study of Southeast Asian herdsmen ants of the genus *Dolichoderus* (DILL, WILLIAMS & MASCHWITZ 2002). The worker of all herdsmen species transport their pseudococcid partners (several genera in the tribe Allomyrmococcini) between their mandibles. In addition to mandible-transport, riding, i.e., the autonomous mounting and clinging to the worker's body, is known to regularly occur in four out of eleven allomyrmococcine genera. Since the riding behaviour can also be observed, at least occasionally, in most of those Allomyrmococcini species that normally are transported exclusively in the ant's mandibles, and given the strong development of sucker-like claw appendages in all species that presumably help the mealybug to hold on to the ant's body, the authors suggest that riding behaviour (phoresis) is an early general behavioural trait in the allomyrmococcine pseudococcids.

Is coccoid transport via phoresis thus a more common phenomenon in ant-mealybug associations than currently recognised? Although mandible-transport of scale insects and other trophobiotic hemipterans is widespread in ants (see extensive review in DILL, WILLIAMS & MASCHWITZ 2002, p.286-291), all unambiguous reports of phoresis involve herdsmen ants of the genus *Dolichoderus* and Allomyrmococcini mealybugs (e.g., REYNE 1954, MASCHWITZ & HÄNEL 1985). To my knowledge, there is only one other case of phoresis in scale insects. In the gall-inducing eriococcid genus *Cystococcus*, the crawlers (first-instar females) are carried out of the maternal gall on the body of their adult brothers (GULLAN & COCKBURN 1986). To sum up, phoresis appears to be generally uncommon in ant-coccoid associations and is, with the possible exception of *Aphomomyrmex*, unknown in plant-ants.

6.4.2. Colony founding

If *Cladomyrma* species do not transport mealybugs on their nuptial flight, how, then, could the foundresses ensure the availability of a food source that is essential throughout the life of the colony? Since some coccoids are parthenogenetic, the arrival of a single female immature scale insect soon after colony initiation may be sufficient to establish a long-term resource for the growing colony, but there is no direct evidence that the scale insects studied here are parthenogenetic.

In all *Cladomyrma* species tested (Fig. 6-2) coccoids were more frequent in advanced than in early stages of foundations, confirming that coccoids arrive on the plant after the foundresses. [The relative ages of the foundations are indicated by the presence or absence of brood or the first cohort of workers, but the absolute ages of each of these foundations are unknown.] The alternative explanation that foundresses had carried the nymphs but failed to rear them in their chambers, is excluded by the fact that all queens observed in the process of founding (alighting on a host or chewing an entrance hole) were free of accompanying coccoids. Thus, independent arrivals of trophobionts prior to the production of brood is not uncommon and may occur as early as within the first few days, or even hours, after colony founding (see below).

As in the majority of ants, colony founding in *Cladomyrma* is independent (without the help of workers) and claustral. New colonies are usually initiated alone (haplometrosis) but cooperative foundings with other foundresses (pleometrosis) possibly occur occasionally in species inhabiting *Neonauclea* trees (less than 0.5% of the foundations dissected contained two living queens together with brood). Newly mated queens select a host plant, seek out an internode offering suitable founding conditions and hollow out the initial nest chamber. The entrance hole is then plugged with masticated pith material.

The sealing of entrance holes is commonly observed in other claustrally founding plant-ants (e.g., FIALA & MASCHWITZ 1990, MASCHWITZ et al. 1996b, CHOE & PERLMAN 1997, YU & DAVIDSON 1997, FEDERLE, MASCHWITZ & FIALA 1998b). This 'closing behaviour' is generally thought to be an important trait to reduce intra- and interspecific competition as well as to avoid attacks by predators and parasitoids. For example, competition among *Cladomyrma* foundresses is intense, with multiple queens initiating colonies in individual saplings and vying for dominance (unpublished results). Strong circumstantial evidence also indicates that young *Cladomyrma* colonies eliminate all other foundresses and natal colonies on the same host. Claustral foundation thus helps the foundress to escape antagonistic interactions with other foundresses or natal colonies. It also may postpone hostile encounters until the incipient colony has developed a sufficient number of workers to persist on its host.

6.4.3. Secondary slits

By this reasoning, the necessary sealing of the entrance hole and the acquisition of trophobionts appear to contradict each other. A plausible option to ensure both safety and access of coccoids simultaneously is to provide openings small enough to exclude alien ants but large enough to allow the passage of immature scale insects. And indeed, founding queens of most *Cladomyrma* species produce such tiny openings, usually less than 1 mm wide. These 'secondary slits' are safely chewed by the foundress from within the initial nest chamber. Size and shape of the narrow oval slits correspond largely to those of nymphal coccoids (Fig. 6-1E, Fig. 6-6A,B).

The results obtained from this study provide evidence that the number of secondary slits significantly and positively correlates with the number of coccoids in founding chambers of *C. petalae* inhabiting *Saraca thaipingensis* (Fig. 6-4). In the *Cladomyrma-Neonauclea* association, however, the difference in the number of secondary slits between founding chambers with and those without coccoids was not significant, although it appeared to follow the same trend (Fig. 6-4). Two factors might explain the dissimilar results.

First, the average number of secondary slits is higher in *Neonauclea* foundations than in those of *Saraca* (mean 8.1 versus 4.0, respectively). Since the number of slits is generally high in *Neonauclea* foundations, a positive effect of additional slits on the number of coccoids in founding chambers may only become apparent in a larger sample. The number of secondary slits in *Cladomyrma-Neonauclea* associations is the highest measured among *Cladomyrma* species, possibly because the slits are, in contrast to all other known *Cladomyrma* host plants, restricted to a thin-walled 'prostoma line' running along each side of the domatium. The chewing of secondary

slits is thus expected to require relatively low energy investment by the foundress compared to their creation in 'normal' internode walls.

Second, and more importantly, the secondary slits may not only serve as entry points for coccoids but might also play a role in regulating microclimatic conditions within founding chambers. *Neonauclea* ant-plants grow predominantly in open disturbed habitats and are usually exposed to high light levels. In consequence, the number of secondary slits may also be a response of the foundress ants to the degree of insulation in order to regulate temperature and/or humidity inside their nest chambers. Therefore, as a first estimate of a possible influence of climatic conditions on slit number, I compared the number of secondary slits produced by *Cladomyrma* foundresses between 'sunny' and 'shady' habitats, but no significant effect of light levels on the number of secondary slits could be found, neither in *C. petalae* nor in the *Cladomyrma-Neonauclea* associations (Fig. 6-3).

However, the rough method applied ('shade' versus 'sun') may be inadequate to detect an influence of chamber microclimate on slit number produced. For example, a high number of slits may reduce nest temperature in exposed habitats but may also aid in drying moist founding chambers created in young soft internodes of plants growing in the shady understorey. In addition, the temperature inside a domatium has been shown to differ from external air temperatures due to factors such as domatia colour, wall thickness, or sun exposure (JANZEN 1967, HOCKING 1970, NETO & ASAKAWA 1978, WHITTEN 1981). The significance of secondary slits for the microclimatic conditions within founding chambers of *Cladomyrma* remains to be tested.

6.4.4. Primary hole

Not all *Cladomyrma* queens gnaw secondary slits. Foundations of the two species *Cladomyrma crypteroniae* and *C. maschwitzi*, both inhabiting the tree *Crypteronia griffithii*, always lack secondary slits. However, coccoid numbers increased with founding stage similarly to those of other *Cladomyrma* species (Fig. 6-2A). The experimental results on primary hole development during the founding stage obtained from *C. maschwitzi* (Fig. 6-7) provide strong evidence that potential coccoid access is ensured by the foundresses which gnaw on growing callus tissue and thus prevent the full closure of the entrance hole for many weeks.

It would be interesting to test whether the maintenance of a slit-like orifice can be influenced by the experimental introduction of coccoid crawlers during the early founding stage. Nevertheless, the regulation of microclimatic conditions by founding

queens might also play an important role in keeping an orifice at the primary hole. Given this reservation, it is to be expected that early acquisition of coccoids may lead to a (nearly) complete closing of the entrance hole to reduce the threat of encounters with competitors, predators and/or parasitoids.

6.4.5. Experimental exclusion of trophobionts

Is the presence of trophobionts essential for the successful rearing of the first cohort of workers in *Cladomyrma*? The experimental exclusion of coccoids from founding chambers of *C. petalae* appears to support this hypothesis (Tab. 6-1). Within the first five to six weeks after founding, all foundations dissected of both the experimental and the control group contained eggs and/or larvae. In the foundations examined after the 6th week, however, the two groups showed contrasting patterns of colony development. In the experimental group, none of the foundresses had produced pupae and workers and although a few larvae were present until the 8th week, eggs were not found after the 6th week. This was in striking contrast to the control group. Workers and pupae were present in all but two foundations examined after the 6th week. Of the two foundations lacking workers and pupae, one also contained no pseudococcids.

One striking result of the study was that all four foundresses in the experimental group collected after the 10th week were found dead. Although this observation appears to corroborate the hypothesis that the acquisition of coccoids during the founding stage is an essential part in the successful establishment of a new colony, it may also weaken the validity of the results obtained in this study if foundress deaths are due to other causes than absence of coccoids and occurred all in the experimental and not the control group simply by chance.

The snapshot method applied in this study does not allow us to determine the date of foundress death. However, two parameters, i.e., chamber length and number of secondary slits, that are usually low in case of the early death of a *Cladomyrma* founding queen, were similar to those of the control group. Each foundation was fully isolated, having no open orifice connecting it to the outside world. Moreover, the foundress corpses were complete and no remains of other arthropods could be detected. These observations combined suggest (i) that death had occurred at least one or two weeks prior to collection and (ii) that parasitoids or predators are not likely to be the cause of foundress death. Parasitoid infestation appears to be generally rare in *Cladomyrma* species. Among hundreds of foundations dissected (n>600) I found only four parasitoids (unidentified flies and braconid wasps).

The assumption that absence of pseudococcids in the experimental group is the most likely explanation for the death of the foundresses seems to be supported by differences in the egg number within the control group. Egg numbers were generally higher in the control than in the experimental group, except when coccoids had not yet been acquired (Tab. 6-1, day 22 and 49). In these cases, egg number was as low as in the experimental group (day 19 to 36), suggesting that the presence of coccoids influences the amount or quality of resources a *Cladomyrma* foundress has for raising her first batch of brood.

A claustrally-founding queen depletes body reserves (flight muscles, fat bodies) to sustain herself and to nurture her first offspring (KELLER & PASSERA 1989, WHEELER 1994). The claustral founding queen has to distribute her limited body reserves among several tasks including nest construction, egg laying, feeding larvae, and maintenance of her own metabolic needs. Under unfavourable conditions, foundresses may be physically exhausted before the emergence of the first cohort of workers (nanitics), or the latter might suffer high mortality due to malnutrition (HÖLLDOBLER & WILSON 1990). The number of nanitics is one of the most important sociometric factors during colony initiation, and it may be fatal if too few nanitics are produced for colony maintenance before the second cohort of workers emerges (OSTER & WILSON 1978, TSCHINKEL 1991).

The number of first workers produced is not fixed but regulated in response to various factors of foundresses such as initial body weight (LIU et al. 2001). The authors demonstrated that claustral founding queens are ready to eat in the founding period, although they normally have no access to food. The claustrally-founding queens of some *Azteca* plant-ant species inhabiting *Cecropia* trees appear to occasionally forage outside their founding chamber, as indicated by the presence of food bodies in 0.5% of the 967 foundations observed (CHOE & PERLMAN 1997). Moreover, artificially fed foundresses of *Camponotus japonicus* significantly layed more first-batch eggs and produced a higher number of nanitics (LIU et al. 2001).

In view of these findings, it seems likely that *Cladomyrma* foundresses benefit from the arrival of trophobionts. First, honeydew is a nutritive mixture of sugars, lipids, amino acids and other nitrogenous products (review in DAVIDSON & PATRELL-KIM 1996, GULLAN & KOSZTARAB 1997). Although the amount of amino acids is low, at least part of the own metabolic costs of the foundress is met, hence more body reserves can be allocated to the production of brood and its nurture. Second, even if the first cohort of workers may be raised successfully without the presence of trophobionts (5% of the *Cladomyrma* foundations with workers lacked coccoids, see

Fig. 6-2), the available honeydew resource is certainly an advantage in the maintenance of the first workers which aid in rearing the second cohort of workers. As discussed above, a foundress which produces a high number of workers early in the initiation of a new colony gains a lead over competing intraspecific colonies and is better equipped to persist on its host. Third, foundresses or natal colonies may not only exploit trophobiotic coccoids for their honeydew, but may also prey upon them when resources are in short supply.

Some plant-ants are known to occasionally prey upon trophobionts (BAILEY 1923, JANZEN 1972, SCHREMMER 1984, FONSECA 1993, MCKEY & MEUNIER 1996), but in many cases the evidence is indirect or doubtful (e.g., WHEELER 1921c, BAILEY 1922b, PFANNES & BAIER 2002). In a study on the *Crematogaster-Macaranga*-coccid associations, ITINO et al. (2001b) claim that ants selectively eat younger coccid nymphs because they observed a skewed age distribution of the coccids. However, such a skewed age distribution may also occur when coccid nymphs leave their parent plant to colonise new host plants. Furthermore, in the same ant-plant-coccid system *Crematogaster* ants were not observed to exploit coccids as a protein source, neither under normal nor starvation conditions (HECKROTH, FIALA & MASCHWITZ 1999). Even if evidence indicates that coccoids are indeed used as a protein source by the ants, it often remains unclear (i) whether only dead or injured scale insects are eaten, (ii) whether living trophobionts are killed and consumed during periods of food shortage, or (iii) whether the ants may actively regulate the size of the coccoid population within the ant colony by killing and feeding on surplus scale insects.

In *Cladomyrma*, evidence for preying upon trophobionts is lacking. HECKROTH (2000; appendix, p. 181) presented preliminary results on *C. petalae* (ex *Saraca*) and two unidentified *Cladomyrma* species (ex *Drypetes*, *Neonauclea*): Workers and larvae collected from mature colonies kept in artificial boxes under starving conditions refused to feed on offered coccids and after three (*Cladomyrma* ex *Drypetes*, *Neonauclea*) and six days (*C. petalae*) almost all workers and larvae had died while several coccids survived the study period. This experiment, however, is not sufficient to generally exclude feeding of trophobionts by *Cladomyrma* because (i) the offered trophobionts were coccids (not pseudococcids), (ii) the artificial conditions of the experimental setup may have prevented 'natural' behavioural responses of the ants, and (iii) ants may behave differently in the founding stage than in the ergonomic or reproductive stage of the colony.

Are other food sources available to foundresses of *Cladomyrma*? Claustrally-founding queens of some plant-ant species are presumed to obtain food within the domatia

directly from the plant in the form of nutritive parenchyma and callus tissue, as in *Cecropia* (IHERING 1907, EIDMANN 1945, DAVIDSON & FISHER 1991) and *Endospermum* (DAHL 1901), or callus alone, as in *Vitex* (BAILEY 1922b). It should be noted, however, that some authors question the hypothesis that parenchyma and callus of *Cecropia* are a critical food source for foundress *Azteca* ants (PERLMAN 1992, CHOE & PERLMAN 1997). Generally, the mere fact that plant tissue is excavated or gnawed by ants does not necessarily indicate that it is actually eaten by them, since it may be removed solely for the purpose of cleaning or enlarging the domatia.

There are no indications that *Cladomyrma* queens utilise any direct plant food sources during colony founding. Excavated pith material is always removed through the entrance hole or used as a plug. Debris resulting from creating secondary slits or smoothing the inner internode walls is deposited as a compact mass at one end of the founding chamber or pushed through the entrance hole. Foundresses chew at callus tissue developing at the hole margins, but I attribute the chewing to efforts (i) to maintain a slit-like orifice (see above), or (ii) to keep the callus thin enough for workers to chew through when they re-open the colony's entrance hole.

How long can *Cladomyrma* foundresses survive in the absence of coccoids and workers? Estimates of foundress survival are only available for *C. petalae* (Tab. 6-1) and *C. maschwitzi* (pers. observation). Living foundresses in chambers containing brood but no coccoids and workers have been found until the 7^{th} and 8^{th} week after founding. These findings possibly reflect the upper limit of survival time. In the presence of coccoids, survival time may be extended, as suggested by a live *C. petalae* queen found with 50 eggs and 3 pseudococcids (but no workers) 65 days after founding (Tab. 6-1). It is proposed that acquisition of trophobionts within the survival limits set by internal and external factors of founding queens (e.g., amount of body reserves, costs of host finding and nest excavation) is either an indispensable condition or at least a major advantage for the successful establishment of a new colony. Depending on arrival time, coccoids may (i) facilitate worker production itself, (ii) enhance the chance to survive until the first workers emerge, or (iii) serve as an immediately available resource for the first workers and thus favour rapid colony development.

In view of the strong intraspecific competition (as is the rule in *Cladomyrma*), rapid colony development is certainly a premium. The importance of an immediately available food resource for the persistence and establishment of new colonies is a general trait in plant-ants (DAVIDSON & FISHER 1991, DAVIDSON & MCKEY 1993). In ant-plants providing their ant partners with specialised food bodies, colonisation of

host saplings by founding queens usually does not occur prior to the production of food (e.g., FIALA & MASCHWITZ 1992b). In the *Piper-Pheidole* mutualism, the only known case where ants induce food body production after arrival, the foundress starts her new colony in a cavity formed by the appressed margins of the petiole and the sheathing leaf bases. It is also the place where food bodies are produced (RISCH et al. 1977, FISCHER et al. 2002). While induction of food body production within a few weeks has been demonstrated for *Pheidole* workers (RISCH & RICKSON 1981), the literature provides no information on whether the foundress induces production of food bodies as well and whether she feeds upon them during the founding stage.

6.4.6. Active entry of immature mealybugs into founding chambers

If trophobionts are as important as proposed above for the establishment of a new colony, all depends on the probability of their acquisition. What is the chance of *Cladomyrma* foundresses to acquire trophobionts? To my knowledge, estimates of the average abundance of immature pseudococcids per given area are lacking for SE Asian tropical rainforests, but it is relatively simple to study behaviour of nymphal mealybugs when encountering a founding chamber of *Cladomyrma* (Fig. 6-5, Tab. 6-2). The ability of immature pseudococcids to enter founding chambers on their own seems to be highly developed. Half of the nymphs (5 of n=10) experimentally placed close to a foundation of *C. petalae* successfully located and entered the nest chamber through one of the secondary slits gnawed by the foundress ant. All the other nymphs tested, except for one, settled in external depressions on the plant surface or hid under adjacent plant structures. If these results based on a low sample size are representative of mealybug behaviour under unmanipulated conditions, access of immatures to foundations may occur with striking ease when nymphs are in proximity to nest chambers. Hence it is not surprising that mealybugs can occasionally be found in *Cladomyrma* foundations within the first few days, and even hours (n=1), after founding takes place.

Active entry of scale insects into nest chambers is possibly a rather common phenomenon in tripartite ant-plant-coccoid associations. In the African ant-plant *Cuviera*, associated with *Crematogaster* ants, coccoids can enter young domatia on their own accord, as indicated by the presence of coccoids in some domatia not yet inhabited by ants but infested by beetle larvae feeding on the remains of dried pith (BEQUAERT 1922). An apparent similar case is reported for the neotropical ant-plant *Tachigali paniculata* (WHEELER 1921). Adult beetles occasionally occupy domatia until they are taken over by plant-ants of the genus *Azteca* or *Pseudomyrmex*. Pseudococcids are found in domatia occupied by beetles prior to the presence of ants and, according to WHEELER (1921), the mealybugs probably begin to enter the

domatia through the openings made by the beetles. In *Cecropia* trees, a small percentage of foundations of *Azteca xanthocroa* and *A. constructor* (still lacking workers) contained pseudococcids (0.21%, n=967), although founding queens do not carry coccoids on their dispersal flight (PERLMAN 1992). Mature colonies usually all tend trophobionts (LONGINO 1991a). In Australia, a presumably host-specific *Camponotus* species inhabits twigs of the mangrove tree *Sonneratia alba* (NIELSEN 2000). None of several hundred founding chambers discovered contained workers, but small coccids of the genus *Myzolecanium* were present in some of the cavities known to be more than six weeks old. Again, virtually all mature colonies contained trophobionts.

In SE Asia, an unidentified arboreal ant species of the genus *Technomyrmex* tending trophobionts inside carton nests built under leaves is also known to acquire coccoids during the founding stage (WEISSFLOG 2001). Seven of ten initial nest chambers found containing a foundress, brood, but no workers, already harboured coccids, while three still lacked trophobionts. In contrast, all colonies (whether natal or mature) encountered with workers tended coccids. The presence of coccids in founding chambers either indicates that coccids migrate into the carton nests by themselves or that foundresses select a site for colony foundation where coccids are already present.

Successive arrival of trophobionts in ant nests, indicating that they get access actively and/or are collected by the first emerging workers, has also been reported for specialised plant-ants. In the SE Asian ant-rattan *Korthalsia robusta*, the *Camponotus* ant partners tend trophobiotic hormaphidids (*Cerataphis* spp.). None of the four foundress queens observed entering a domatium carried a trophobiont in their mandibles (MATTES et al. 1998). Nevertheless, of nine foundress queens checked for the presence of *Cerataphis* in their ocrea domatia, only one lacked its aphid associate, indicating that the establishment of trophobionts appears to take place rather early during colony initiation of *Camponotus* on *Korthalsia robusta*. In the myrmecophyte *Macaranga lamellata*, associated with both *Camponotus macarangae* and *Crematogaster* sp., coccids were found in 46% of the *Camponotus* colonies, and in 65% of the *Crematogaster* colonies. Foundresses of both species, however, were never found with soft scales (MASCHWITZ et al. 1996b). Similarly, in the African plant-ant *Tetraponera aethiops* inhabiting domatia of *Barteria fistulosa*, foundresses with few progeny were not accompanied by coccoids, while established colonies appear to depend totally on the honeydew excretions of the trophobionts (YUMOTO & MARUHASHI 1999).

To sum up, acquisition of trophobiotic scale insects (or hormaphidids in ant-rattans) appears to occur relatively early in all obligate tripartite ant-plant-trophobiont associations for which information on trophobiont access is available. From the ant's point of view, several possible behavioural traits facilitate access of coccoids during the founding stage: (i) foundresses carry coccoids either in their mandibles or phoretically, (ii) founding queens maintain entrances for nymphal coccoids which are capable of entering nest chambers on their own, and (iii) the first workers leaving the initial nest chamber and foraging on the plant surface collect and transport coccoids into their nest.

6.4.7. Scale insect dispersal

With the exception of active or passive coccoid-carrying by a foundress ant whereby scale insects from the maternal nest are transferred to the new nest site, all other strategies of colony founding require that coccoids independently arrive at or are already present on the new host plant. How do scale insects disperse? The main dispersal agents in the Coccoidea are first instar nymphs, the so-called crawlers (review in GULLAN & KOSZTARAB 1997). Crawlers are passively dispersed by wind, although mortality is high. Several morphological and behavioural adaptations for aerial dispersal in crawlers have been suggested, e.g., comparatively long legs and antennae in relation to body size, downwind orientation, and even standing on hind legs with legs outstretched to become launched (WASHBURN & WASHBURN 1984, HANKS & DENNO 1993). Wind-dispersed crawlers usually cross distances of a few metres to kilometres, although rarely some may be carried for several hundred kilometres. Wandering is another dispersal option available to scale insects and may be initiated in the absence of suitable feeding sites (WASHBURN &. FRANKIE 1985).

In a SE Asian lowland rainforest, estimates of 'crawler rain', i.e., number of wind-dispersed coccid crawlers arriving on a given area per unit of time, are provided by HECKROTH (2000). Thirteen coccid-free seedlings of the ant-plant *Macaranga hullettii* (artificially colonised with *Crematogaster* ants) were distributed in the Pasoh Forest Reserve (Malaysia) in at least 30 m distance to adult *Macaranga* plants. Colonisation by coccids from the ground was prevented with sticky resin applied around the seedling stem. Coccid number relative to leaf area was measured after 44 days and the mean colonisation rate was calculated as roughly one crawler per m^2 leaf area and week or, if production of crawlers is constant throughout the year, as over 500,000 crawlers per hectare leaf area and year. These estimates only include coccids tended by *Crematogaster* plant-ants on *Macaranga* hosts but the total amount of coccoid crawlers floating through the air may be considerably higher.

On occasion, wind dispersal of immature mealybugs from *Cladomyrma* host plants could be observed. On a sunny day at about 13.00 h, a pseudococcid crawler left a hollow chamber in a twig of the tree *Saraca thaipingensis* (Malay Peninsula), then walked about five centimetres on the upper surface of the internode, raised its forelegs and suddenly was launched from the twig as the observer felt a slight breeze. Samples collected from the interior of the cavity were identified as *Planococcus lilacinus* and *Crenicoccus gullanae* (D. J. WILLIAMS, pers. communication), indicating that the crawler probably belonged to one of these two species. On a sunny day at 11.30 and 12.30 h, two dispersal events have been observed on pseudococcids leaving the domatia of the ant-plant *Neonauclea gigantea* (Sabah, Borneo). On each of two *Neonauclea* trees inhabited by *Cladomyrma*, a single immature mealybug (> 1 mm length, second instar?) left a domatium, walked some centimetres, stopped shortly and was blown away by a breeze.

To acquire coccoids, it is not necessary that wind-dispersed crawlers directly alight close to a founding chamber. Several other factors combined also enhance the possibility of coccoid access to ant foundations. First, seedlings may already accumulate coccids before reaching a size suitable for ant colonisation. Second, developmental time of coccoids is short, e.g., coccids of the *Crematogaster-Macaranga* association reach maturity within 40 to 44 days (HECKROTH 2000). Third, newly produced crawlers often settle on the natal host when conditions are favourable (GULLAN & KOSZTARAB 1997) and, instead of being dispersed by the wind, crawlers may only wander on the plant to search for a new feeding site, hence they potentially encounter a founding chamber. Fourth, the first cohort of workers may collect immature coccoids on the plant surface and incorporate them into their colony. The latter has been demonstrated for the *Crematogaster-Macaranga*-coccid association (HECKROTH 2000).

6.4.8. Conclusion

Despite the risky nature of dispersal of coccoids by wind, the chance of scale insect acquisition during the founding stage is presumably better for many plant-ants than recognised by previous studies (GAUME, MATILE-FERRERO & MCKEY 2000). Although intriguing, co-dispersal, i.e., the vertical transmission of both ant and coccoid, is a rarely realised option for plant-ants to successfully establish a colony on a new host plant. Instead, plant-ants and coccoids commonly disperse independently from each other (horizontal transmission). During the founding stage, the maintenance of small slits permitting the entry of immature coccoids seems to be an important behavioural trait in *Cladomyrma* ants that increases the chance of coccoid access. Trophobionts

appear to play an important, if not indispensable, role in the success of *Cladomyrma* colony foundation, at least in *C. petalae*.

Future research should clarify the importance of trophobiont presence relative to stage of foundation among *Cladomyrma* species as well as the role of secondary slits for the microclimatic conditions within the founding chamber. Further studies may answer the question why coccids generally arrive later in *Cladomyrma* colonies than pseudococcids, a phenomenon that has also been described for the African plant-ant *Aphomomyrmex* (GAUME & MCKEY 1998). This 'late arrival' of coccids may either reflect different dispersal strategies of soft scales and mealybugs or is due to a selection process by the ant foundress which might prefer pseudococcids over coccids during the founding stage. Finally, studies should specifically examine why colonies of most *Cladomyrma* species are predominantly associated with pseudococcids and others (*C. maschwitzi*) with coccids.

7. Flood control

7.1. INTRODUCTION

The flooding of nest sites is a serious hazard for ants. Survival mechanisms for terrestrial and subterranean ants nesting in regularly or irregularly inundated environments are reported to include high submersion tolerance, 'raft forming', nest moving, sealing of nest entrances, re-excavation of nest chambers, and nest designs facilitating drainage of seeping water (ADIS 1984, MAJER & DELABIE 1994, PEETERS et al. 1994, NIELSEN 1997 and 2000, DIETRICH et al. 1998, ELDRIDGE & MYERS 1998, GREEN, PETTRY & SWITZER 1999, LUDE; REICH & PLACHTER 1999). For arboreal nesting ants of perhumid tropical rainforests, heavy showers pose an unpredictable threat. Construction of nests built of, or attached to, 'waterproof' leaves is a common phenomenon (e.g. HÖLLDOBLER & WILSON 1983, BLACK 1987, DOROW, MASCHWITZ & RAPP 1990), but little information is available on the flood control behaviours of arboreal ants nesting in plant cavities.

The removal of water from nest chambers by 'spitting' has been reported in a pseudomyrmecine ant species, *Tetraponera binghami* (as *T.* near *attenuata* PSW-80) living in bamboo internodes (KLEIN, MASCHWITZ & KOVAC 1993, DAVISON 1995). The *Tetraponera* workers remove any rainwater that collects in the internode by licking up the moisture and regurgitating it to the outside from the entrance hole. Other means of flood control by ants include the carrying of water droplets adhering to their body (FEDERLE, MASCHWITZ & FIALA 1998b) and the reduction of water inflow by blocking the nest entrance with their heads (JANZEN 1967, SCHELLERICH-KAADEN et al. 1997a). Recently, a striking new mode of flood control has been reported for *Cataulacus muticus* inhabiting the hollow culms of giant bamboo in Malaysia (MASCHWITZ & MOOG 2000). The ants display a 'communal peeing' behaviour; they respond to nest flooding by drinking the water, leaving the nest and excreting water droplets on the outer stem surface.

Heavy showers in the everwet tropics pose a threat especially for arboreal insects which can be washed down from trees or may even drown in their shelters. Foundress queens of the plant-ant genus *Cladomyrma*, which have to bite nest chambers into their host plant stems for colony foundation, frequently disappear during heavy rain or sometimes drown when seeking refuge in their unfinished, still unclosed chambers due to runoff-water which collects in the hollow internodes via the entrance holes. Mature colonies of these ant species face the same problem of intruding rainwater

endangering ant brood and trophobiotic mealybugs. As obligate plant-ants, *Cladomyrma* species are completely dependent on the integrity of their host plants, hence a colony inevitably dies when the host is destroyed or becomes unsuitable as a nesting site. This immediately raises the question whether *Cladomyrma* has developed behavioural traits that reduce the risk of drowning inside the hollow stems and twigs after nest flooding. Here, I tested how several different species of *Cladomyrma* respond to water collecting in their nest chambers.

7.2. MATERIAL AND METHODS

Nest structure: *Cladomyrma* ants gnaw open the host plant internodes and hollow them out by removing the pith. With both increasing plant and colony size other internodes will be colonised successively. Eventually the nest chambers run through stem, branches and every twig of the host. These hollows contain brood and trophobiotic pseudococcids which are cultivated by the ants. As a rule one nest entrance per plant internode is found, except for *Neonauclea* where the number of entrance holes per domatium varies, usually from four to six, depending on both domatium and colony size. In all host plants the entrances are situated more or less at the lateral sides of the internodes. Thus the risk of getting runoff-water into the nest chambers is reduced (except for the vertical stem). However, there may still be a considerable amount of seepage. I longitudinally dissected several inhabited internodes of the trees *Saraca*, *Ryparosa*, *Neonauclea*, *Crypteronia*, and the woody climber *Spatholobus*. By watering the outer walls of the internodes I could check from inside that small amounts of water do intrude into the nest. However, the runoff water sometimes passes the entrances due to very small callus ridges around the holes. Rain water may also penetrate into the nest hollows through openings of damaged twigs, the latter being torn open by predators of ants and brood.

To test how *Cladomyrma* ants react to the intrusion of water I injected between 0.2 and 6 ml water, stained with non-poisonous, water-soluble food coloring, into nest entrances with a syringe. In total, I performed 16 tests with nine colonies of three *Cladomyrma* species, *C. dianeae* (1 colony: 3 tests), *C. maschwitzi* (4 col.: 6 tests), *C. petalae* (4 col.: 7 tests), in nine host plants of five different species: *Saraca thaipingensis* (n=2), *Ryparosa fasciculata* (n=1), *Spatholobus bracteolatus* (n=1), *Crypteronia griffithii* (n=4), and *Neonauclea gigantea* (n=1).

On each plant the experimental twigs were fixed in a horizontal position to prevent the injected water from draining away inside the nest channels. Prior to injecting coloured

liquid, I fixed a small filter paper (4 x 4 cm) beneath each experimental entrance hole (n=16). The observation period of the ant's behaviour lasted at least one hour (see table 7-1 for details). The following parameters were measured: (i) increase in ant activity at the affected area after start of the experiment, (ii) time of first appearance of workers with distended gaster indicating that the ants drank the experimentally injected water (tested by squashing a few workers between filter paper), (iii) time of first observation of workers that bail out water, (iv) droplet-ejection frequency per two successive 10-min counting intervals, and (v) number of droplets on the plant surface or on filter paper placed beneath entrance holes.

7.3. RESULTS

Table 7-1 summarises the results. Within minutes after the experimental flooding of the internodes (range 1 to 15 min, median 4, mean 5.38 ± 4,76 SD) the number of workers increased noticeably (at least three-fold compared to activity level prior to injection) around the affected areas. Shortly afterwards the first workers with distended gasters, containing coloured liquid, appeared on the plant surface (range 3 to 65 min, median 5, mean 12.08 ± 17.52 SD). After ingesting the water the workers regurgitated droplets and either smeared them onto the stem surface or dropped them off the plant. On average, the first water-ejection behaviour occurred after 24.92 min ± 13.18 SD (range 3 to 41, median 27).

The results are highly variable and may be due to (i) different amount used of injected liquid, (ii) the number of workers involved, i.e., colony size, (iii) incomparability of risk levels, i.e., different number of larvae or pseudococcids inside the affected internodes, and (iv) species-specific differences in behavioural response. However, if we look separately at 'increased activity' (ia) and first observation of 'water-bailing' (wb) for three categories of amount of injected liquid (0.2 ml; 2 ml; 3–6 ml, resp.) the median values may indicate a tendency for an accelerated behavioural response of the *Cladomyrma* workers to an experimental increase of water injection: *for 0.2 ml*: 12.5 min ia versus 28.5 min wb; *for 2 ml*: 2.5 min ia versus 5 min wb; *for 3–6 ml*: 2.5 min ia versus 31.5 min wb.

Table 7-1: Response of *Cladomyrma* species, colonising different host plants, to experimentally injected liquid (artificially coloured) into inhabited internodes. Columns: *increased activity* = time after injection until an increase in worker numbers (at least three-fold) on plant surface was observed; *distendend gaster* = time of first occurence of workers with distended gaster on plant surface; *water-bailing* = time of first observation of workers that bail out water; *ejection frequency* = droplet-ejection frequency per 10-min counting interval (first 10-min; following 10-min); *liquid-filled crops* = crop of workers filled with coloured liquid, tested by squashing worker gasters between filter paper. *Neo* = *Neonauclea gigantea*; *Sar* = *Saraca thaipingensis*; *Spa* = *Spatholobus bracteolatus*; *Ryp* = *Ryparosa fasciculata*; *Cry* = *Crypteronia griffithii*; y = yes; n = no; ? = not recorded.

	ant colony	observation period [h]	amount injected liquid [ml]	increased activity [min]	distended gaster [min]	water-bailing [min]	ejection frequency [droplets/10-min]	liquid-filled crops	droplets found on plant surface	droplets found on filter paper	workers observed ingesting liquid
C.dianeae/Neo	#1	2	2	3	3	5	58; 108	y	y	y	n
		2	2	2	3	3	78; 76	y	y	y	n
		2	2	1	4	4	?	y	y	y	n
C.petalae/Sar	#2	2	4	4	5	21	?	y	y	n	n
		2	6	1	3	27	?	y	y	n	y
		3.5	6	1	5	n	?	y	y	n	y
	#3	2	2	7	8	39	44; 58	y	y	n	n
C.petalae/Spa	#4	2	3	6	17	36	40; 76	y	y	y	n
		2	3	4	9	41	51; 112	y	y	n	n
C.petalae/Ryp	#5	1	6	1	4	n	?	y	y	n	y
C.maschwitzi/Cry	#6	2	2	1	65	n	?	y	y	n	n
	#7	1	2	5	19	35	25; 35	y	y	y	n
	#8	1	0.2	10	?	25	?	?	y	y	?
		1	0.2	14	?	31	?	?	y	y	?
	#9	1	0.2	15	?	27	?	?	y	y	?
		1	0.2	11	?	30	?	?	y	y	?

The latter value seems to contradict this statement but I interpret this 'delay' of water-removal as the consequence of massive flooding of the nest channels. As confirmed by direct observation of dissected twigs, workers drowned in water need up to several minutes to escape from the flooded internode. After cleaning themselves, they may even try to get back into the flooded area in order to safe their brood.

In three tests (19%) the water-bailing behaviour could not be observed directly (see table 7-1). However, both workers with liquid-filled crops and droplets on the plant surface were found, demonstrating that ingestion and subsequent regurgitation had taken place. Furthermore, in two of these three experiments the ingestion could be directly observed (*Saraca* and *Ryparosa*). While the workers were circled around the

entrance hole, putting in their heads alternately, the increasing distension of the gasters was clearly visible.

In all *Cladomyrma* species, the majority of workers involved in water-bailing activity appear in the entrance hole, often protruding up to the alitrunk or even gaster, and press out a droplet until it reaches about the size of their head. Then, the droplet is dropped off or smeared around the entrance hole, resulting in a typical wet spot at the affected area (Fig. 7-1).

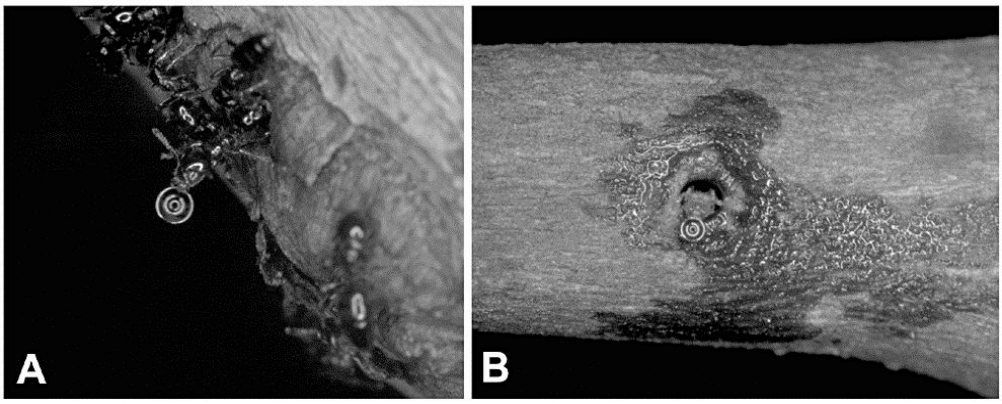


Figure 7-1: Water-bailing of *Cladomyrma*. **A**: *C. dianeae* in *Neonauclea gigantea*; diameter of droplet ca. 0.9 mm; **B**: *C. maschwitzi* in *Crypteronia griffithii*; diameter of droplet ca. 0.6 mm.

In six experiments the droplet-ejection frequency was counted per two successive 10-min intervals (Tab. 7-1). The frequency varied from 25 to 112 droplets per 10-min (median 58, mean 63.42 ± 27.47) and increased from the first 10-min counting interval to the second (1: median 47.5, mean 49.33 ± 17.93; 2: median 76, mean 77.5 ± 29.36). During the 2 hours of continuous observation the droplet-ejection frequency remained on a rather high level and did not decrease markedly. However, during spot checks after 9 h (*C. dianeae* in *Neonauclea*, *C. petalae* in *Saraca*) and 24 h (*C. maschwitzi* in *Crypteronia*) no water-bailing activity was registered, indicating that the injected liquid had been removed. Subsequent dissection of the experimental internodes confirmed the complete removal of the injected liquid.

An estimate of the water-bailing capacity of the ants was derived from number and average volume of the ejected water droplets. Judging from photographs, the average droplet diameter is approximately equivalent to the head length of major and minor workers respectively, i.e., ca. 1.2 and 0.8 mm for both *C. dianeae* and *C. petalae* and ca. 1.0 and 0.6 mm for *C. maschwitzi*. The proportion of major and minor workers involved in removing water was not measured, therefore the mean diameter of major

and minor workers is used. These estimates correspond to an average droplet volume of 0.52 μl for *C. dianeae*, *C. petalae* and 0.27 μl for *C. maschwitzi*. At the observed average ejection frequency of ca. 6 droplets/min, 10.7 h (for *C. dianeae*, *C. petalae*) and 20.6 h (for *C. maschwitzi*) would be required to remove the experimentally injected 2 ml. These results roughly agree with the observation of ceased water-bailing activity after 9 and 24 h respectively.

7.3.1. Summary of the results: flood control

- after experimental flooding of the nest chambers with water, the number of workers increased at the affected area in all *Cladomyrma* species tested (*dianeae*, *maschwitzi*, *petalae*)
- shortly afterwards the workers drank the injected water
- workers of all species tested regurgitated droplets and dropped them off the plant or smeared them onto the stem surface
- the water-bailing behaviour continued for hours until no standing water remained inside the nest chambers

7.4. DISCUSSION

Until now *Cladomyrma* species are the only mutualistic plant-ants known to drain their host cavities as described above. It is not yet known how other plant mutualists avoid damage due to water intrusion, except for an undescribed formicine *Camponotus* (*Colobopsis*) plant-ant species. In the latter, the workers coming out of experimentally flooded internodes of myrmecophytic *Macaranga puncticulata* carried water droplets adhering between their legs on the body underside. The ants probably also drink the injected water but water-bailing has not been observed (FEDERLE, MASCHWITZ & FIALA 1998b). Though the response of *Camponotus* to nest flooding appears to be rather 'unspecific', the ants managed to remove the injected water completely out of their domatia within one day.

Preliminary data on *Crematogaster* (subgenus *Decacrema*) species which are obligate tenants of *Macaranga* spp. in SE Asia indicate that these ants do not bail water out of their domatia. I tested the response of three *Crematogaster* morphospecies, associated with *M. bancana* (Miq.) Muell. Arg. (n=5), *M. hullettii* King ex Hook. f. (n=1), and *M. hosei* King ex Hook. f. (n=1) to the flooding of their internodes. During 5 hours of observation neither water-bailing behaviour nor droplets on the plant surface or filter paper could be registered.

The only other ant species exhibiting water-removal behaviour were reported in the pseudomyrmecine *Tetraponera binghami* and in the myrmicine *Cataulacus muticus*. These two species exclusively inhabit the hollow living culms of giant bamboo but they are looked upon as being more likely parasitic than mutualistic associates of giant bamboo (BUSCHINGER, KLEIN & MASCHWITZ 1994, MASCHWITZ et al. 2000). The hollow bamboo culm segments are especially prone to flooding because (i) many internodes are punctured by stem-boring insects, and (ii) stem flow of rainwater during heavy rains is intense. The resulting water-bodies (phytotelmata) found within the bamboo internodes are inhabited by a rich fauna of limnic and terrestrial arthropods (KOVAC & STREIT 1996).

Tetraponera binghami keeps its internodial nests in the culms dry in the same mode as *Cladomyrma*, i.e., the ants lick up the water and 'spit' the regurgitated droplets out of their nest chambers (KLEIN, MASCHWITZ & KOVAC 1993). The other bamboo specialist, *Cataulacus muticus,* exhibits a peculiar water-bailing behaviour not previously reported for any other ant species (MASCHWITZ & MOOG 2000). The ants drink the water, leave the nest and excrete water droplets on the outer stem surface. During heavy rains, workers of both bamboo-dwelling species also reduce water influx by blocking the entrance holes with their heads (KOVAC 1994, MASCHWITZ & MOOG 2000). This two-graded response to flooding –first 'sealing', then 'spitting' or 'peeing'– enables *Tetraponera* and *Cataulacus* to utilise the hollow bamboo culms as long-lived, secure nesting and feeding site.

The workers of a third ant species, *Polyrhachis schellerichae*, which is another non-mutualistic associate of giant bamboo, also block the nest entrance with their heads during rain and thus reduce inflow of rain water. They do not, however, bail out water from their nest internodes, and small amounts of water are sometimes found inside the nest chambers (SCHELLERICH-KAADEN et al. 1997a). It remains to be tested if *Polyrhachis* is more effective than *Tetraponera* or *Cataulacus* in sealing the nest entrance against intruding rainwater.

The use of both water transport and fanning to cool overheated nests is a common phenomenon in social bees and wasps (WILSON 1971). Moistening of the nest has also been observed in the ant *Pseudomyrmex mexicanus* (KLEIN, MASCHWITZ & KOVAC 1993). The opposite behaviour, removing moisture from the nest, is also known in social Hymenoptera. Workers of the wasp species *Polistes acutiscutis* and *Polybia occidentalis* suck water from the wet nest surface and regurgitate it to the outside (JEANNE 1991). In tropical arboreal ants, this behaviour is virtually unknown. The examples presented above are mostly from ants specialised to living in giant bamboo.

This is not surprising because the amount of rainwater flowing down the vertical smooth culms during rain is intense and thus ants require behavioural traits that reduce or prevent flooding of their nest internodes.

Although the capability of water-removal appears to be of major importance in specialised bamboo-nesting ants, it is unclear if behavioural traits that reduce the risk of nest flooding are equally important in other arboreal ants. A commonly realised solution of arboreal ants for escaping the threats of heavy rains in tropical rainforests is to construct nests build of, or attached to, 'waterproof' leaves (e.g. BLACK 1987, DOROW, MASCHWITZ & RAPP 1990, WEISSFLOG 2001). In twig-nesting ants, however, the risk of drowning or suffering unsuitable nesting conditions due to excess moisture has rarely been investigated. In *Echinopla* sp., for instance, living in polydomous colonies in the hollows of dead twigs, water-removal could not be provoked (A. REICHARDT, pers. comm.). After water-injection the workers left their nest chambers, trying to smear off adhering water, and moved to another nest site.

Emigration to other nest sites, a generally observed behavioural response of ants to nest disturbance (e.g. WILSON 1986a), is not possible for obligate plant-ants like *Cladomyrma*. They rely entirely on their host plant, which provides shelter and nutrition via honeydew of trophobionts. *Cladomyrma* colonies never leave their host and will die together with their ant-plant if the latter is destroyed. The water-bailing behaviour seems to be an effective countermeasure to flooding, especially for initial colonies which inhabit only few internodes. Here, runoff water that collects in the nest chamber may not only threatens some brood and trophobiotic mealybugs but also endanger colony development as a whole. Further investigation is required to show if other arboreal twig-dwelling ant species have developed specific mechanisms which allow them to live in habitats where heavy rains and floods are common phenomena.

8. Ant activity

8.1. INTRODUCTION

In many ant/plant associations, the ants exhibit a preference, in varying degrees, in their patrolling activity on external plant surfaces by concentrating on young foliage (e.g., JANZEN 1967 and 1972, DOWNHOWER 1975, RISCH 1982, STOUT 1979, FIALA & MASCHWITZ 1990, MADDEN & YOUNG 1992, FONSECA 1994, FEDERLE, MASCHWITZ & FIALA 1998b, COGNI & FREITAS 2002, IZZO & VASCONCELOS 2002, THURNER & MAYER 2008, MOOG et al. 2008). This concentration of ant activity on young plant parts is often achieved by restricting the production of resources such as extrafloral nectar or food bodies to young, vulnerable leaves.

In some protective ant-plant mutualisms, however, the patrolling activity appears to be decoupled from the distribution of food sources offered by the plant. For example, the African myrmecophytic tree *Leonardoxa africana* subsp. *africana* provides extrafloral nectar as the principal or sole food source of the plant's host-specific ant mutualist, *Petalomyrmex phylax* (MCKEY 1984, GAUME & MCKEY 1999). The nectaries at the base of each leaflet become active, and are visited by ants, only after the leaf matures. Nectar production –and hence ant visitation of nectaries on mature leaves– is concentrated during a brief period around mid-day. In contrast, patrolling of leaf surfaces by *Petalomyrmex* is completely restricted to tender young leaves, the entire surface of the leaf is patrolled, and patrolling is continuous over day and night and throughout development of the young leaf.

Are other food resources the cause for the spatially clumped patrolling activity of the ants? It appears that many specialist plant-ants do not (or rarely) eat the insects they encounter on young leaves (JANZEN 1967, FIALA et al. 1989, FONSECA 1993, GAUME, MCKEY & ANSTETT 1997, AGRAWAL 1998, GAUME & MCKEY 1998; but see DEJEAN et al. 2009), but rather simply chase them off or discard them from the leaves. Thus, in most specific ant-plant systems, ants do not concentrate their activities on young leaves because they obtain more insect food there. The majority of ant-plant symbioses involve hemipteran trophobionts as a third partner, and it is widely assumed that food provided either directly by the plant or via trophobionts is sufficient to supply a complete diet for the associated plant-ant colony (DAVIDSON & MCKEY 1993a, and references therein). This possibly explains why insects encountered on young leaves are relatively unimportant as a food resource for the plant's specific associates.

From the plant's point of view, a colony of plant-ants is costly since the colony is usually maintained by resources obtained, either directly or indirectly, from the host plant. Thus, selection should favour allocation of biotic defence, i.e., of the ant worker force, either to plant parts where herbivore damage would have the greatest impact on plant fitness, or to those parts that are most likely to be attacked by herbivores (BROUAT et al. 2000). In other words, plant parts less valuable and/or vulnerable should be ignored by the mutualistic ants.

In this study, I examine whether *Cladomyrma* species exhibit a preference in their patrolling activity for certain plant parts. More specifically, I asked the following questions: (1) Do the host plants of *Cladomyrma* produce food bodies or extrafloral nectar on their surface, especially on young leaves, that may attract ants? (2) Do the activity patterns of the ants differ spatially, i.e., among plant parts, and/or temporarily between day and night?

8.2. MATERIALS AND METHODS

Food rewards on the plant surface?

To test whether host plants produce food bodies and/or extrafloral nectar on their outer surface that may serve as ant attractants, I selected three to ten twigs with both immature and mature leaves of each host plant species and isolated them from ant access by applying insect glue (Tangle-trap, Tanglefoot Corp., Grand Rapids, Mich., USA). In addition, two to five twigs of each host species, likewise bearing different aged leaves, were enveloped with a gauze net to exclude flying nectar consumers and to allow accumulation of nectar droplets. Ant entrances along the twigs were plugged with glue. The following plants were tested:

host plant taxa	*n* twigs with insect glue	*n* twigs with gauze net	*n* plants
Callerya nieuwenhuisii	5	3	5
Crypteronia griffithii	10	5	10
Drypetes longifolia	6	3	5
Luvunga sp.	3	2	5
Neonauclea gigantea	6	3	5
Ryparosa fasciculata	3	3	5
Saraca thaipingensis	10	5	10
Spatholobus bracteolatus	3	2	3
Strychnos vanprukii	4	2	6

After three days the twigs and leaves were closely examined for the presence of food bodies or foliar nectar.

Spatial and temporal distribution of ant activity

In order to provide a cross-section of the temporal and spatial activity patterns of the *Cladomyrma* ants on their host, I performed several censuses differing in the following aspects:

1.) Hourly counts during three successive days (65 h): Ant activity of a *Cladomyrma petalae* colony inhabiting the tree *Saraca thaipingensis* was recorded concurrently with measurements of temperature and relative humidity. In three previously selected areas on the tree, I counted the number of ants on the plant surface every hour. These census areas consisted of (i) 2 young leaf flushes and the associated 2 successive internodes of each leaf flush, (ii) 2 older leaf flushes plus 1 associated internode, and (iii) a branch section, 30 cm long, with mature leaves. Each census area had roughly the same length. For observations conducted at night a red-filtered head lamp was used in order not to disturb the ants.

2.) Hourly counts during a 24-h cycle: A total of five *Cladomyrma maschwitzi* colonies inhabiting *Crypteronia griffithii* were censused in 1-h-intervals over a 24-h cycle. Counts were performed at three twigs per plant (in total n=15 twigs). I chose twigs with both immature and mature leaves and counted the number of ants on (i) immature apical leaf pair plus associated internode, (ii) first subapical mature leaf pair plus internode, and (iii) second subapical mature leaf pair plus internode.

3.) Spot checks: I performed spot checks on several additional *Cladomyrma* species to estimate if the spatial and/or temporal activity patterns obtained from the 24-h-cycle censuses are shared among the *Cladomyrma* species. As in the previous counts I selected twigs with both immature and mature leaves and scored the number of ants on successive plant parts. Each census area consisted of a leaf (or leaf pair) and the associated internode. On ant species level, counts were scattered over several days and daytimes, however, night observations are lacking for *C. crypteroniae* and *C. hobbyi*. For a few colonies of each species more than one count per day was taken; in these cases at least one hour elapsed before the next count.

taxa ant - host plant	*n* counts	*n* colonies
Cladomyrma andrei - Callerya nieuwenhuisii	24	8
Cladomyrma crypteroniae - Crypteronia griffithii	7	4
Cladomyrma hobbyi - Spatholobus oblongifolius	15	9
Cladomyrma petalae - Saraca thaipingensis	62	6 *
Cladomyrma yongi - Drypetes longifolia	18	14
Cladomyrma sp. ** - *Neonauclea gigantea*	21	13

* these colonies do not include the colony used in the continuous 3-day-census (see above).
** mostly *C. dianeae* but perhaps *C. maryatiae* as well (four colonies?).

Data analysis

The spatial distribution of ant activity was analysed with the nonparametric Friedman-test for multiple paired samples, because each twig gave data repeatedly for a dependent variable (*Ho*: There is no effect of the plant part on ant activity). The temporal distribution of ants was only analysed for the 24-h censuses, i.e., for *Cladomyrma petale* and *C. maschwitzi*. First, I calculated the mean number of ants for each census time (n=24 hours) and colony, and then tested for homogeneity using the Chi Square test. All tests were run in StatView 4.51 for Macintosh (Abacus Concepts, Inc., Berkeley, California, USA).

8.3. RESULTS

8.3.1. Food rewards on the plant surface?

With the exception of *Saraca thaipingensis*, none of the host plant species tested in exclusion experiments produced visible food rewards on the leaf or twig surface. Neither food bodies nor accumulation of extrafloral nectar (droplets) were observed. In the host plant genera *Neonauclea* and *Spatholobus*, however, I tested only one host species each for food rewards offered on the plant surface. For the remaining known *Cladomyrma* host species belonging to these two genera, namely *Spatholobus oblongifolius* and seven other *Neonauclea* species, circumstantial evidence indicates that food rewards are lacking as well. First, examination of the leaf surfaces revealed no structures resembling nectaries. Second, in uninhabited plants of *Neonauclea* no visiting ants were observed foraging regularly on the leaves (mostly at leaf base or leaf margin) as is typical for extrafloral nectary-bearing plants. Third, in plants of both *Spatholobus* and *Neonauclea*, I never observed *Cladomyrma* ants feeding on structures such as food bodies or nectaries.

The tree *Saraca thaipingensis* stands out among host plants of *Cladomyrma* by having extrafloral nectaries along the margins of its leaflets. Usually one functional nectary is situated at the base of the leaflet, and two additional nectaries occur at the apex of the leaflet (near the drip-tip). They are active only in young developing leaves, and a variety of ants and other hymenopterans have been observed to feed on the secretions (Fig. 8-1). They include species of the ant genera *Camponotus*, *Crematogaster*, *Gnamptogenys*, *Prenolepis*, *Rhoptromyrmex*, *Tapinoma*, and *Technomyrmex* as well as *Trigona* stingless bees and eumenid wasps. Sugar concentration of the extrafloral nectar is high; tests for glucose with dextrostix (Merck) yielded the max. possible reading of ≥ 2.5 g/l.

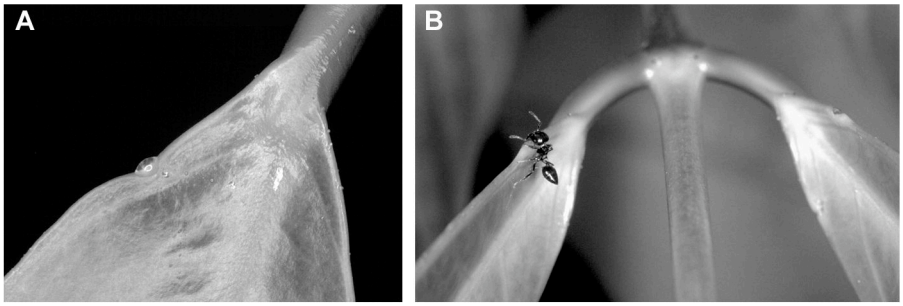
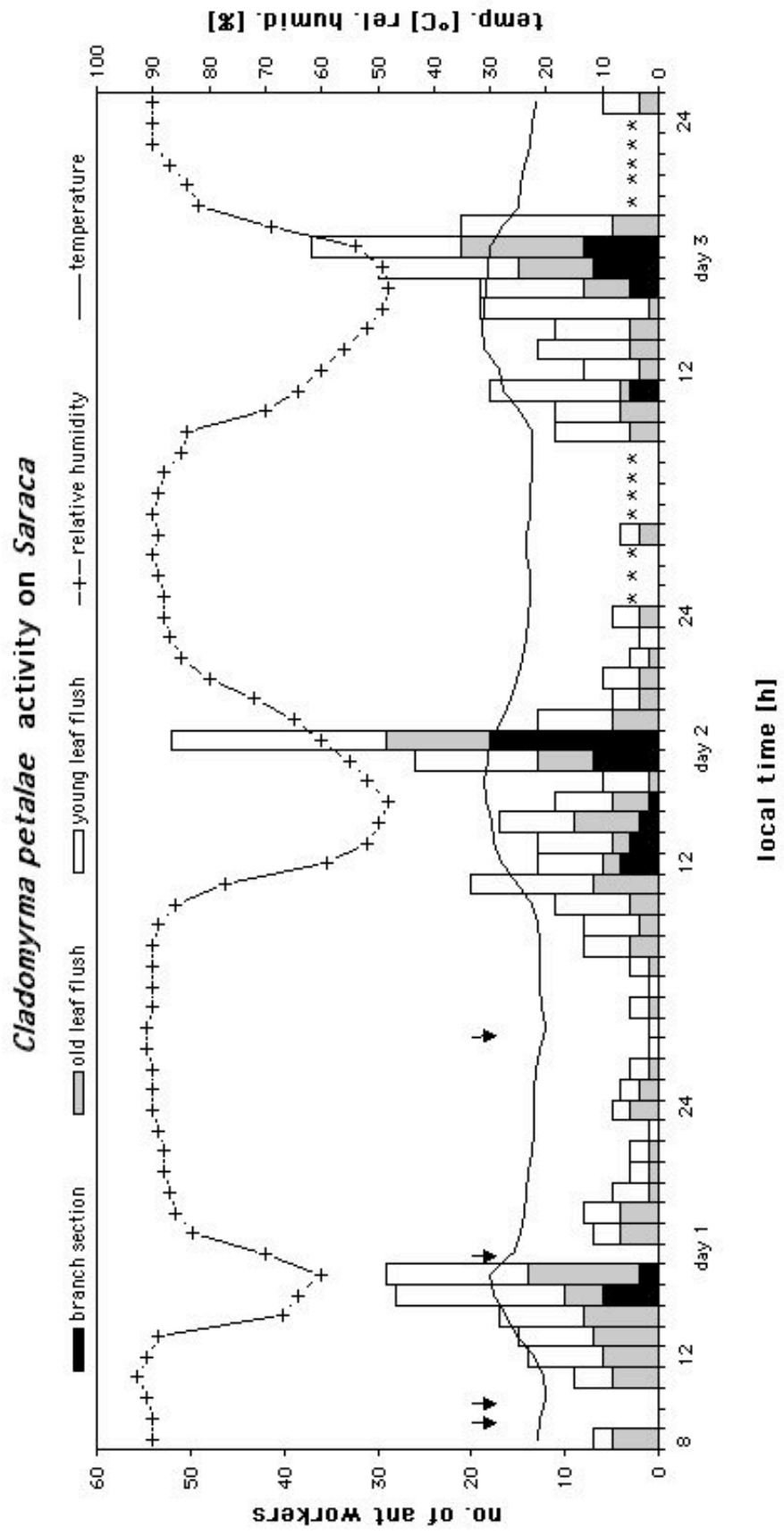


Figure 8-1: Extrafloral nectaries of *Saraca thaipingensis*. **A**: nectary with accumulated nectar droplet at base of young leaflet. **B**: worker of *Crematogaster* sp. harvesting extrafloral nectar. The nectary at the opposite leaflet has already been visited by the worker.

Opportunistic 'tourist' ants visiting extrafloral nectaries typically move along the leaf margins and check extrafloral nectaries for accumulated droplets. However, I have never seen *Cladomyrma* workers examining the nectaries for nectar supply although I spent countless hours on observation. Also, nectar accumulation was not observed on leaves of *Saraca* hosts colonised by *Cladomyrma*. This suggests that nectar secretion is reduced in *Cladomyrma*-inhabited plants, perhaps mediated by lack of harvest and subsequent drying up of the first nectar produced. Only in colonies experimentally set to starvation by cutting the stem of the host plant (thus disconnecting the trophobiotic scale insects from their phloem supply) were *Cladomyrma* workers induced to harvest extrafloral nectar from uninhabited *Saraca* plants to which the original host was tied.

Figure 8-2 (next page): Activity pattern of a *Cladomyrma petalae* colony on a *Saraca thaipingensis* tree during a continuous 3-day period. The number of ant workers was recorded hourly for three census areas of different age but roughly the same length (young and old leaf flush, branch section). *Arrows*: periods of rainfall. *Asterisks*: missing data.


Cladomyrma petalae activity on Saraca
branch section
old leaf flush
young leaf flush
relative humidity
temperature
no. of ant workers
temp. [°C] rel. humid. [%]
local time [h]
day 1
day 2
day 3

8.3.2. Spatial and temporal distribution of ant activity

1.) Hourly counts during three successive days (65 h): Number of *Cladomyrma petalae* workers on a *Saraca thaipingensis* tree was recorded at plant parts of different ages. Figure 8-2 describes the pattern of ant activity in relation to temperature and relative humidity.

During the 3-d period three main patterns are immediately apparent. First, ant number increased during the day and reached its peak at times of low relative humidity and high temperature sometime between mid-day and afternoon. [The high number of ants (52) counted on the second day at 18.00 h is in part due to an alarm recruitment caused by my unintentional touching of a leaf flush; without this artefact ant number is estimated to be approx. 40 workers.] Ant activity distinctly decreased at dusk (~19.30 h). The differences in mean activity level during a 24-h cycle are highly significant (test for homogeneity, chi square = 69.08, df = 23, $P < 0.0001$). Second, ant number rarely dropped to naught, even at night one or few workers stayed on the plant surface. At night checks I usually found the ants motionless on the underside of immature leaflets. Third, young plant parts (leaf flushes and associated internodes) were preferred over older plant sections and activity on branches was restricted to relatively short periods during the day. Ant activity was also strongly affected by weather conditions. On the first day of the observation period heavy rainfall caused the ants to hide in their nest cavities (Fig. 8-2). Additional observations at other times suggest that ants may stay on the plant surface when rainfall is relatively weak.

The patterns observed appear to be consistent from day to day, however, this short-term study allows no generalisation. Do these patterns hold if more colonies of *C. petalae* are included? Do other *Cladomyrma* species show a similar pattern? In the following I will focus on these questions.

2.) I censused ant activity of five *Cladomyrma maschwitzi* colonies hourly over a 24-h cycle. Counts included three twigs per plant (*Crypteronia griffithii*) and each twig included both immature and mature leaf pairs. Figure 8-3 shows the mean ant number of all data pooled. As in the previous observation on *C. petalae* the *C. maschwitzi* ants exhibited a preference for the younger plant parts. They also showed a temporal preference in their activity on the plant surface for daytime, reaching a peak in the afternoon. The differences in mean activity level during the 24-h cycle are highly significant (test for homogeneity, chi square = 61.16, df = 23, $P < 0.0001$). This result is true for the pooled data, however, ant number varied considerably among twigs occupied by the same colony.

An extreme example is presented in figure 8-4, serving as a good reminder to be cautious in drawing conclusions from a small sample. Here, activity on one twig was restricted to daytime, whereas activity on another twig, occupied by the same colony, was seen only at night. The causes for this variation are unknown. As a consequence of this variation in activity levels, single twigs may be free of patrolling ants for a considerable period of time, probably over several hours (although I cannot exclude that ant workers were present between the hourly counting intervals).

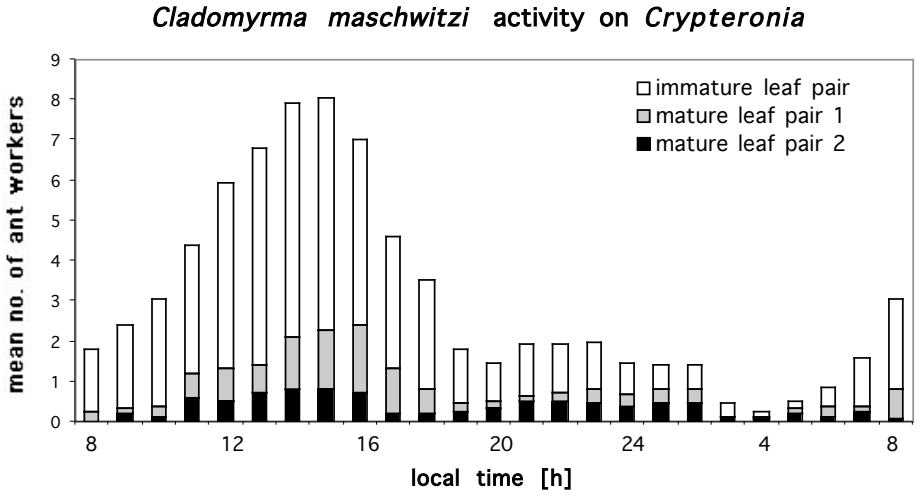


Figure 8-3: Mean number of *C. maschwitzi* workers on the surface of *Crypteronia griffithii* during a 24-h cycle (pooled data; n = 5 colonies).

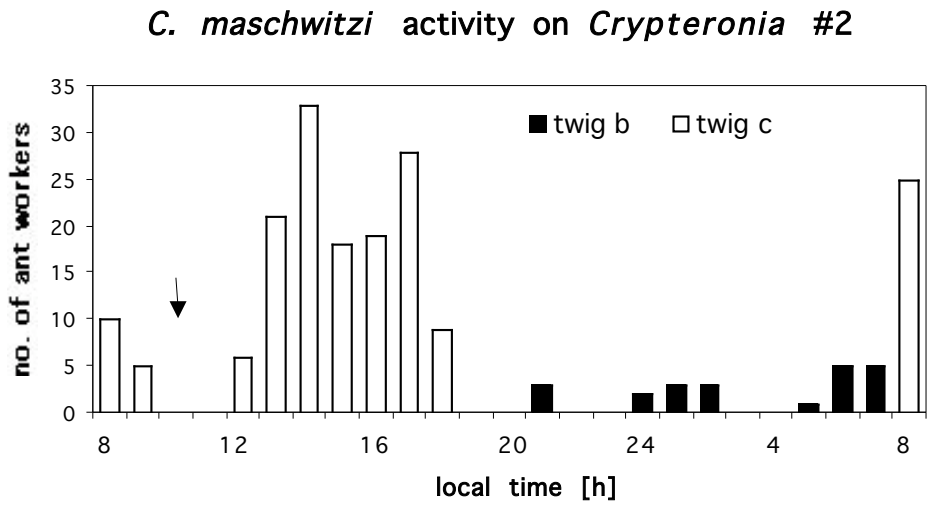


Figure 8-4: Variation among twigs in external activity of a *C. maschwitzi* colony on *Crypteronia griffithii* #2 during a 24-h cycle. For more clarity, twig a, showing the more general pattern as seen in figure 8-3, is omitted. *Arrow*: rainfall period.

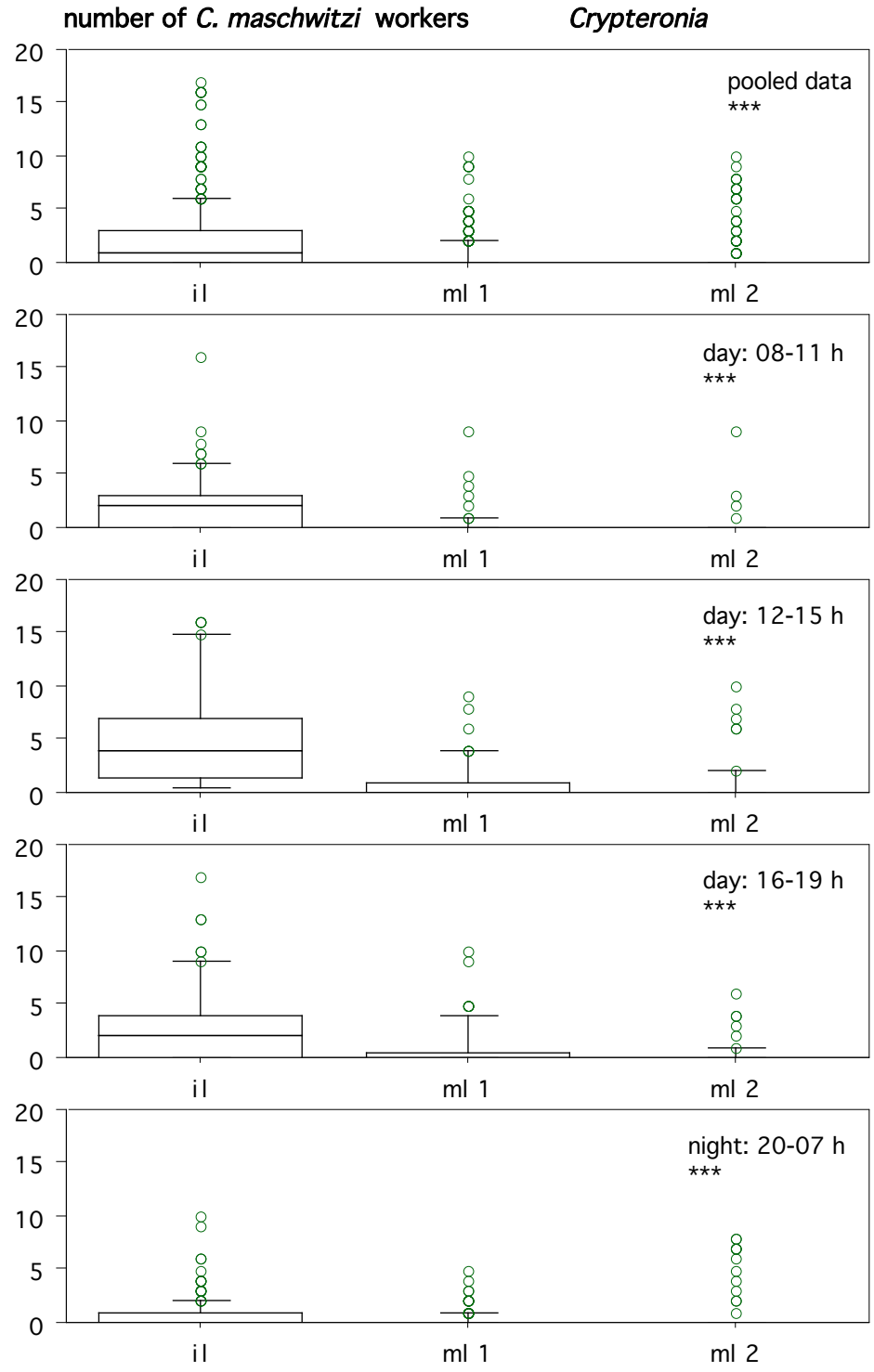


Figure 8-5: Spatial distribution of *C. maschwitzi* ants on *Crypteronia griffithii* for all data pooled (top chart) and for a given day period. *il* = immature leaf pair plus associated internode; *ml 1* and *ml 2* = mature leaf pair plus internode in subsequent order along the twig. Data are based on 24-h censuses of five colonies, with counts performed on three twigs per plant and colony. In all cases differences in ant numbers between plant parts are highly significant (Friedman's test, $P < 0.0001$). [For explanation of box-whisker plots see figure 4-45.]

The spatial distribution of *Cladomyrma maschwitzi* workers on the surface of *Crypteronia griffithii* was strongly biased –independent of daytime– towards young, immature plant parts (Fig. 8-5). On average, 2.2 workers were present on any young immature leaf pair and its associated internode (median 1.0; n=375 counts). Although ant activity is distinctly lower during the night (20-07 h: mean 0.74 ± 1.46 SD) as compared to daytime (e.g., 12–15 h: mean 5.4 ± 5.48 SD), in all cases differences in ant numbers between the three subsequent plant parts were highly significant (non-parametric Friedman's test for comparison of multiple paired samples, $df = 2$, $P < 0.0001$).

3.) Spot checks on several additional *Cladomyrma* species were performed to estimate if the spatial and temporal activity patterns obtained from the 24-h-cycle censuses are shared among the *Cladomyrma* species. As in the previous counts, I selected twigs with both immature and mature leaves and scored the number of ants on successive plant parts.

Cladomyrma petalae on *Saraca thaipingensis*: The results obtained from the spot checks (based on six colonies, n=62 counts) are, in principle, comparable to those obtained both from the 3-d census of *C. petalae* and the 24-h censuses of *C. maschitzi* (see above): young leaves and shoots are preferred over older plant parts and this preference remains constant independently of daytime (Fig. 8-6). This difference in spatial distribution was highly significant for the pooled data and all time periods tested (Friedman's test, $df = 5$, $P < 0.0001$). In addition, night activity is lower compared to day activity and the highest numbers of ants are observed in the afternoon (12–15 h and 15–19 h), thus corroborating the findings of the 3-d census.

In contrast to *C. maschwitzi*, the average number of *C. petalae* ants on immature leaves was almost five times higher (mean 10.68 ± 9.32 SD). But since the spot checks were not evenly distributed over the day and included only 11 night counts (versus 52 daytime counts), the average number of *C. petalae* ants is biased towards daylight activity levels. Thus a direct comparison of the mean ant number between *Cladomyrma* species is misleading. However, since the intention of the spot checks was to measure both the spatial distribution of a given *Cladomyrma* species on its host and the relative change of activity level during the day *within* a species (and not to compare activity levels *between* species) this procedure is justified.

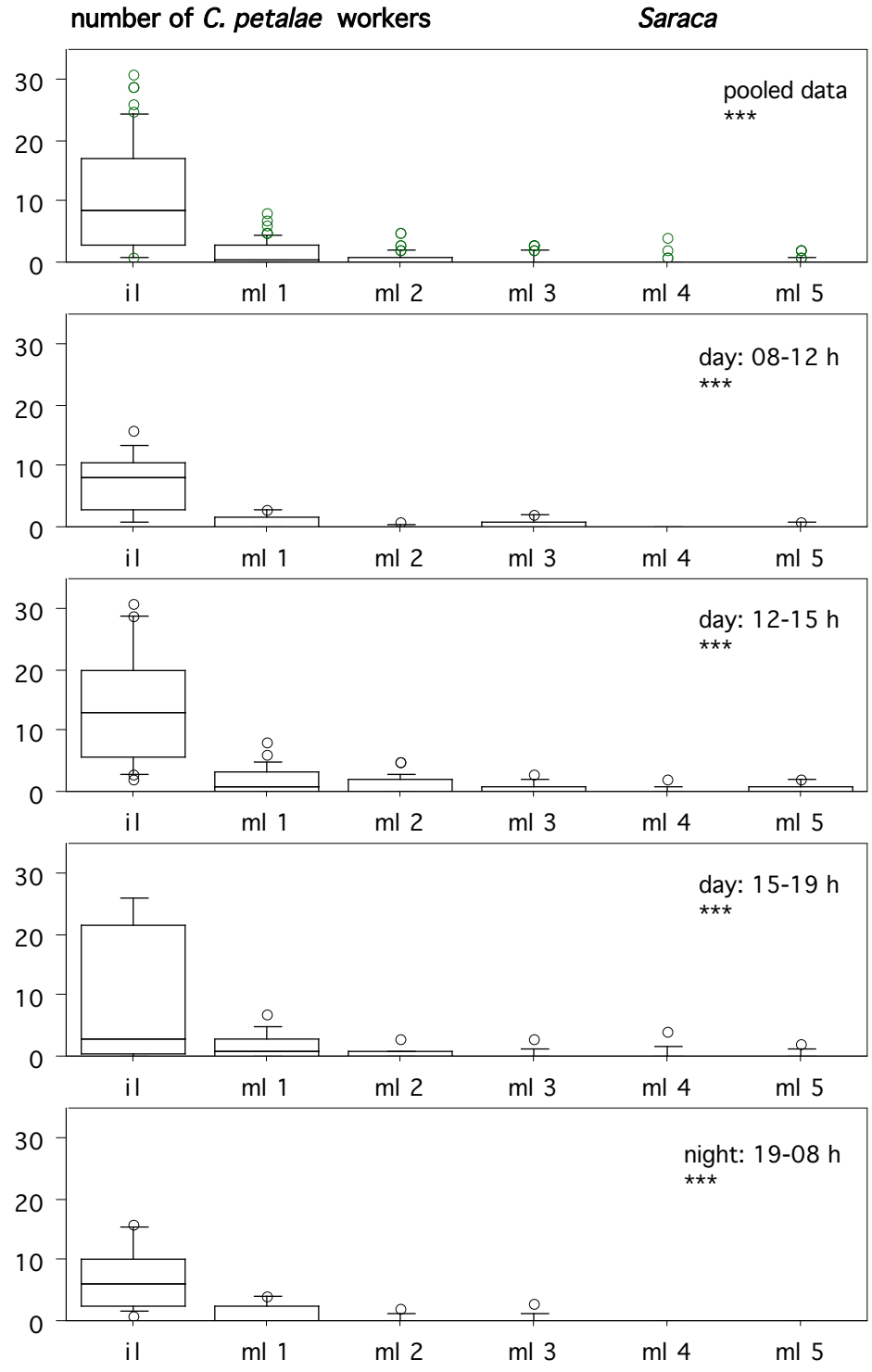


Figure 8-6: Spatial distribution of *C. petalae* ants on *Saraca thaipingensis* for all data pooled (top chart) and for a given day period. *il* = immature, apical leaf plus associated internode; *ml 1* to *ml 5* = mature leaves plus associated internode in subsequent order along the twig (from apical to basal). Data are based on spot checks of six colonies, with a total of 62 counts performed on 19 different days. In all cases differences in ant numbers between plant parts are highly significant (Friedman's test, $P < 0.0001$***). [For explanation of box-whisker plots see figure 4-45.]

In addition to *Saraca thaipingensis*, *Cladomyrma petalae* inhabits several other sympatric host plant species, i.e., *Ryparosa fasciculata*, *Spatholobus bracteolatus*, *Strychnos vanprukii*, and *Luvunga* sp. In all these host plant species field observations indicate that the ants show a similar activity pattern with a strong preference for young leaves and shoots (Fig. 8-7).

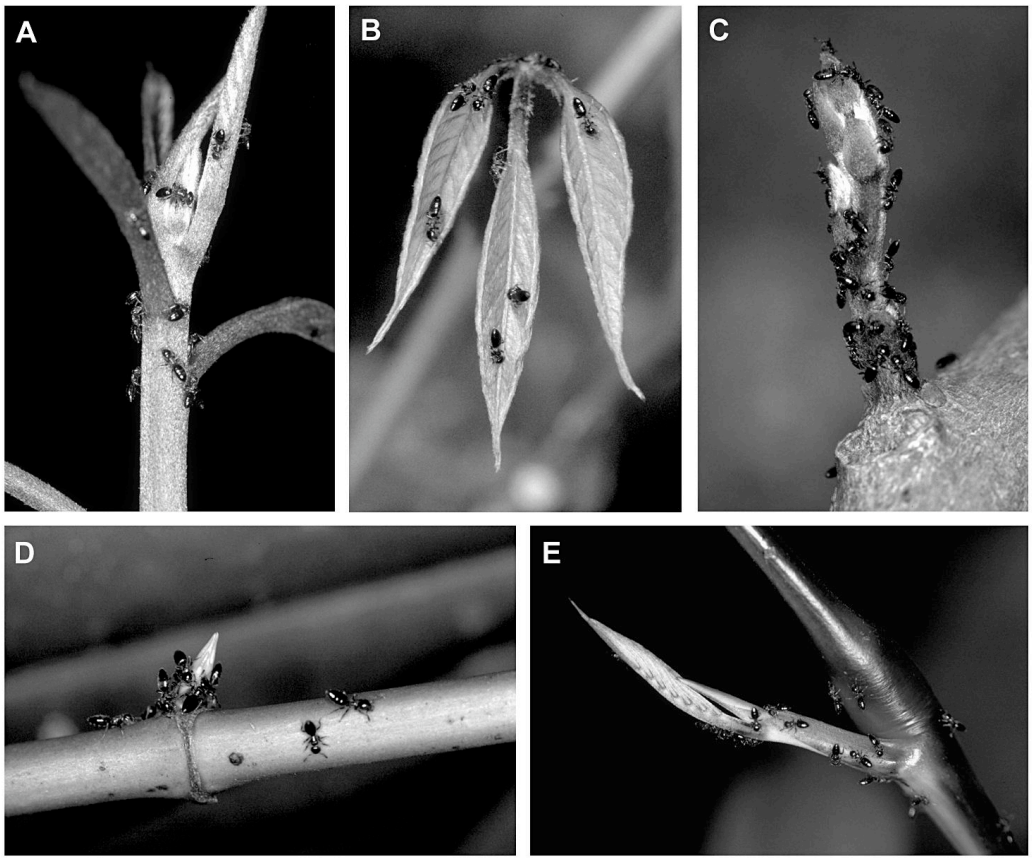


Figure 8-7: Preference of *Cladomyrma petalae* in its external activity for young developing shoots or leaves. **A**: on *Ryparosa fasciculata* (Achariaceae, formerly Flacourtiaceae); **B** and **C**: on *Spatholobus bracteolatus* (Fabaceae); **D**: on *Strychnos vanprukii* (Loganiaceae); **E**: on *Saraca thaipingensis* (Fabaceae).

Cladomyrma spp. on diverse host species: The emerging patterns of ant activity resemble those of *C. petalae* and *C. maschwitzi* (Fig. 8-8). Despite differences in number of new leaves and internodes produced in each spurt of growth among host species, the spatial distribution of *Cladomyrma* ants is consistently concentrated on young, immature plant parts. Differences in ant numbers between plant parts are significant in all cases (Friedman's test, $P < 0.0001$, and $P < 0.001$ for *Cladomyrma crypteroniae* (Fig. 8-8E) due to low sample size and an unusually high ant presence level on a mature leaf pair (ml 1) at one occasion).

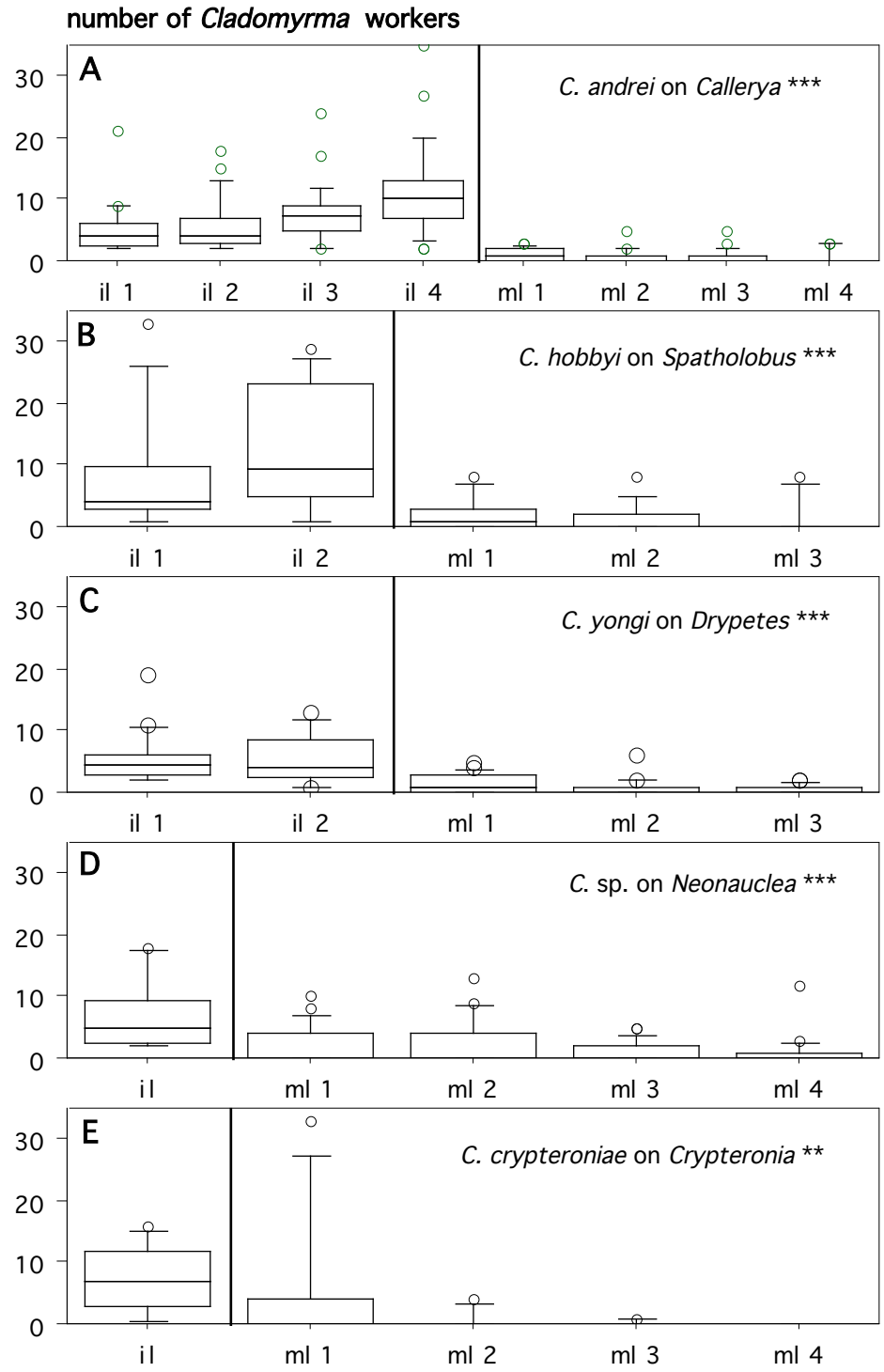


Figure 8-8: Spatial distribution of *Cladomyrma* ants on different plant parts of several host species. *il* = immature, apical leaf (or leaf pair) plus associated internode; *ml* = mature leaf (or leaf pair) plus associated internode in successive order along the twig (from apical to basal). Data are based on spot checks. In all cases differences in ant numbers between plant parts are significant (Friedman's test, $P < 0.0001$*** or $P < 0.001$**). For more clarity, in each graph a vertical line separates the immature and mature plant parts. [For explanation of box-whisker plots see figure 4-45.]

The two *Cladomyrma* species, *C. andrei* and *C. hobbyi*, inhabiting the woody climbers *Callerya nieuwenhuisii* and *Spatholobus oblongifolius* respectively, tend to prefer the relatively 'older' parts of a new spurt of growth (Fig. 8-8A, B). This is presumably due to the greater diameter of the 'lower' new internodes compared to the most apical ones, often the former are strongly swollen (domatia) and thus suitable for colonisation. Here the ants are able to establish new nesting space by hollowing out the internode.

Ant numbers on the plant surface were also distinctly lower at night compared to daylight hours in all *Cladomyrma* species for which nightly counts were conducted, i.e., *C. andrei*, *C. yongi*, *C. dianeae* (or *C. maryatiae*). [Night observations are lacking for *C. crypteroniae* and *C. hobbyi*.]

8.3.3. Activity on mature plant parts

Ant numbers on mature leaves and internodes of the host *Neonauclea gigantea* are slightly greater compared to most other host plant species (Fig. 8-8D; mean 2.24 for both ml 1 and ml 2). Although the numbers of ants are not directly comparable between species (see above) I assume that the architectural characteristics of *Neonauclea* may influence ant activity levels measured on mature plant parts. In contrast to all other host plants where ants live inside continuously hollowed-out twigs (at least in adult plants), the ants' nesting space in adult *Neonauclea* is restricted to the swollen domatia which are separated by several internodes. Therefore, the ants must cross a certain distance on the plant surface in order to reach newly developing leaves.

Most of the day all *Cladomyrma* species studied do not patrol the surface of old plant structures. The low mean ant numbers on mature plant parts result from long periods of zero activity and short intervals of rather high activity. This is exemplified in the 3-d census of *C. petalae* (Fig. 8-2). Such 'outbursts of activity' are usually restricted to stem internodes bearing mature leaves rather than to the mature leaves themselves. During these intervals at least part of the ant workers present on the outer surface of the stems appear to examine the internodes closely, especially at spots where stem wounds are present or where climbers touch the stem. [Pruning behaviour is treated in a separate chapter, 10, p. 282.] In very few cases I have seen the ants carrying brood and scale insects. During these intervals of stem surface activity a greater portion of the host plant's internodes is covered with ants (Fig. 8-9). Periods of activity on stem sections are short (*c*. 1–2 hours) but presumably occur regularly each day.

Figure 8-9: *Cladomyrma petalae* workers patrolling a twig of their host *Ryparosa fasciculata* (tree 4.6 m tall, R-038).

8.3.4. Behaviour of the ants on young leaves

All *Cladomyrma* species, including those for which no activity measurements were taken, patrol young leaves in a characteristic and stereotyped way. Patrolling workers walk constantly but slowly over the entire leaf surface, stopping at intervals for brief periods, while appearing to survey or licking the surface thoroughly. Each worker showed this behaviour continuously over at least several minutes, although the surfaces of the leaves appeared 'clean'. If larger particles such as pith or leaf litter remains were encountered the ants discarded them from the surface. [Tests on 'cleaning behaviour' of *Cladomyrma* by using termite eggs placed on young foliage is presented in chapter 9, p. 232.]

8.3.5. Response to disturbance of the host plant

As a rule, mature colonies of *Cladomyrma* displayed an aggressive behaviour if their host was violently disturbed, e.g., when the plant stem was dissected. In the latter case, major workers hidden in the clothes sometimes searched for and bit into any tender spot of a myrmecologist even two hours after he had broken up the nest and left the site of his crime. In addition to biting the ants simultaneously sprayed formic acid. Fortunately, the bites –even those of the larger *Cladomyrma* species– usually do not break the human skin and the pain is bearable.

Less severe disturbance also caused a response of the ants. According to field observations all *Cladomyrma* species strongly reacted to shaking impulses of their host plant. After applying a shaking impulse (bending down a twig by ca. 45° and releasing it) the number of ants immediately increased on the stem and on the young

leaves (if present). Within several minutes their activity calmed down to normal levels. The response could be provoked at any time of the day, even at night, but intensity of the ants' reaction appeared to be a function of colony size. Bigger colonies responded with a stronger recruitment on the affected twig. Also, recruitment could be released by knocking on the stem. The ants, however, did not react at all when their host plants were only shaken by the wind.

Host plant injuries: Circumstantial evidence indicates that *Cladomyrma* ants react to injuries of their host plant (tested in *C. maschwitzi*, *C. petalae*, *C. yongi*). When leaves where cautiously cut in order to avoid any vibration (n=15) the workers usually detected the wound within several minutes (or seconds, depending on previous activity level) and gathered around the cut, the mouth parts and the antennae being in contact with the plant sap. Ant numbers at the cut varied from one to six and after about three to ten minutes the interest of the ants in the inflicted injury decreased markedly. It is noteworthy that I observed a similar interest in host plant injuries in colony-founding *Cladomyrma* queens. When they encountered a cut during their check of the suitability of an internode for colonisation (n=7) they appeared agitated (as indicated by their increased speed) and inspected the wound closely, whereby changing position several times. After leaving the wound to continue their 'internode check' they often returned to the injury and repeated their former behaviour.

8.3.6. Summary of the results: ant activity

- workers of all *Cladomyrma* species studied show a strong spatial preference for young developing plant parts, independent of time of day or host plant species
- the attraction to young shoots and leaves is not mediated by visible food rewards such as food bodies or extrafloral nectaries (EFN). The nectaries of *Saraca thaipingensis* do not specifically attract *Cladomyrma petalae* ants and *C. petalae* shows the same preference for young plant structures on host plants lacking EFN
- in all species for which night observations are available activity levels are consistently lower at night than during daylight hours; however, number of ants may vary considerably, sometimes even between twigs inhabited by the same colony
- activity is not totally restricted to young plant structures. Patrolling of the stem surface appears to be a behaviour displayed in short but regular intervals by all *Cladomyrma* species investigated
- after disturbance of the host plant, either by shaking a twig or cutting a leaf, the ants respond by increasing their numbers on the affected area
- heavy rainfall causes *Cladomyrma* ants to cease their activity on the plant surface and to hide inside their nest cavities

8.4. DISCUSSION

Cladomyrma is a 'typical' plant-ant with respect to activity patterns on the host surface: (i) the workers are mainly diurnal but maintain a 'night watch', (ii) they respond to disturbance with alarm recruitment to the affected area (after the colony has reached a critical size of at least several dozen workers), and (iii) they patrol the host regularly, strongly preferring young over old plant parts.

8.4.1. Variation of ant activity and response to disturbance

Irrespective of the species tested, the overall activity of *Cladomyrma* on young leaves was more or less permanent, usually with high activity levels during the day (including a peak in the afternoon) and relatively low ones at night, thus resembling the pattern reported for African *Tetraponera* inhabiting myrmecophytic *Barteria* trees (JANZEN 1972). Temporal inter- and, especially, intra-colony variation in *Cladomyrma*'s worker activity was sometimes surprisingly high. For example, worker activity of one colony of *C. maschwitzi*, counted at three twigs of its host tree during a 24-h cycle, varied strongly between focal twigs (Fig. 8-4). Whereas the temporal distribution of workers on one twig resembled the general pattern, the activity on the other two twigs was either strictly diurnal or nocturnal. Although I cannot provide plausible hypotheses for this intra-colony variation, it illustrates that single twigs within a crown may sometimes be free of patrolling ants. As a consequence of this variability in activity levels, herbivorous insects may occasionally be able to feed on young leaves for a considerable period of time without the interference of ants.

Variability in intensity of ant patrolling may be related to, e.g., colony age, colony size (absolute number of workers), density of occupation (colony size relative to host plant size), or weather conditions. Rainfall was found to be an important factor reducing *Cladomyrma*'s patrolling activity. During heavy rain the workers disappear into the safety of their hollow twigs or, if on 'night watch', sometimes hide between the limply hanging leaflets of a leaf flush (*Saraca*). Then, considerable disturbance is necessary to bring workers out of their hiding place. There is ample evidence that rain events generally reduce ant patrolling, not only in plant-ants (e.g., JANZEN 1967, ACKONOR 1984, VASCONCELOS 1991, WIRTH & LEAL 2001, PFANNES & BAIER 2002).

Encounters with phytophagous insects on young plant tissue induced aggressive recruitment of *Cladomyrma* workers. [This ant response is treated separately in chapter 9.] The mobile, rapidly deployable nature of the ants may explain why activity levels can be distinctly lower at night than during the day. Any nocturnal herbivore feeding on the new leaves of a host plant of *Cladomyrma* still risks detection and

attack by defending ants. Recruitment could also be released by shaking impulses of twigs or knocking on the stem, a response to disturbance typical for the majority of plant-ants (e.g., FIALA & MASCHWITZ 1990, AGRAWAL 1998, CRONIN 1998, FEDERLE, MASCHWITZ & FIALA 1998b, GAUME & MCKEY 1999, DEJEAN et al. 2009).

8.4.2. Activity on mature plant parts

Most of the day all *Cladomyrma* species studied do not patrol the surface of old plant structures. They may show, however, short intervals of rather high activity, with columns of workers moving up and down the stem. These 'outbursts of activity' presumably occur regularly each day. During these intervals workers survey the exposed surface closely and probe into corners. They appear to be especially interested in spots where stem wounds are present or where climbers touch the stem. If the workers encounter foreign particles or loose bark pieces on the stem they throw them off the plant. In very few cases I have seen some ants carrying brood and scale insects, but the rarity of this behaviour indicates that it cannot be the sole cause of activity on the stem surface.

In most host plants of *Cladomyrma* the stems and twigs are, at least in adult plants, hollowed out throughout their length, thus connecting the entire nest chamber (disconnected nest parts are rare and can usually be bridged by crossing the surface of one internode only). This allows nest maintenance, such as dispersal of food, brood and scale insects, to take place within the safety of the hollow stems. The situation is different in young saplings of *Callerya*, *Drypetes*, and *Spatholobus*, and in adult *Neonauclea*. Here, the colony lives in a series of dispersed domatia with exposed routes connecting them. This might explain the slightly higher ant activity on mature plant parts observed in *Neonauclea gigantea* (Fig. 8-8D). What is, then, the main function of activity on mature stems? All available evidence indicates that 'pruning' (trimming of alien vines) and 'cleaning' behaviour of *Cladomyrma* are likely important factors for the observed mature-stem activity. [Cleaning and pruning are treated in separate chapters, 9 and 10, p. 239 and 282.]

8.4.3. Preference for young plant parts

The concentration of ant activity on intact young, vulnerable plant parts is a striking phenomenon shared among many plant-ants (e.g., *Alllomerus*: GRANGIER et al. 2008; *Aphomomyrmex*: GAUME & MCKEY 1998; *Azteca*: DOWNHOWER 1975; *Camponotus*: FEDERLE, MASCHWITZ & FIALA 1998b; *Crematogaster*: FIALA & MASCHWITZ 1990, MADDEN & YOUNG 1992; *Petalomyrmex*: MCKEY 1984, GAUME & MCKEY 1999; *Pheidole*: RISCH 1982; *Pseudomyrmex*: JANZEN 1967, FONSECA 1994; *Tetraponera*: JANZEN 1972). Because it is such a widespread and, with respect to biotic defence

theory (see below}, obviously fundamental trait in plant-ants it seems justified to create an easily remembered term for this characteristic behaviour. I propose to call it ***neophily*** (greek *néos* = new, young; *philos* = friend, loving).

Neophily can be achieved by providing dietary resources such as extrafloral nectar (EFN) or food bodies (FB) on young leaves (as in many facultative ant-plant interactions, e.g., RICKSON & RICKSON 1998), but in several obligate ant-plant mutualisms the distribution of ant patrolling appears to be decoupled from the distribution of food rewards (GAUME, MCKEY & ANSTETT 1997). Other food resources, e.g., insects encountered on young leaves, may also influence the distribution of the ants on the plant. However, many specialist plant-ants do not (or rarely) eat the insects they encounter on young leaves (e.g., JANZEN 1967, FIALA et al. 1989, FONSECA 1993, AGRAWAL 1998, GAUME & MCKEY 1998).

The plant-ant *Cladomyrma* is not an exception. This study revealed that *Cladomyrma*'s preference in its patrolling activity for young plant tissue is not caused by obvious food rewards such as EFN or FB. Additionally, *Cladomyrma* ants either chase off or discard herbivorous insects from the leaves (see chapter 9), indicating that these insects do not play an important role in their diet. Hence, insect food is not a likely cause for the concentration of the ants' activity on young plant tissue.

The functioning of ant-plant protection mutualisms should be strongly influenced by the optimal allocation of ants to valuable and/or vulnerable plant parts. As BROUAT et al. (2000; p. 350) have stressed, the plant's colony of mutualistic ant-guards is usually maintained (either directly or indirectly) by resources obtained from the host plant, and thus "selection should favour plant traits that cause ants to patrol those parts that are most likely to be attacked by herbivores or those parts where herbivore attack would have the greatest impact on plant fitness."

8.4.4. Does the host plant mediates the ant's behaviour by chemical signals?

That plants are capable of manipulating ant behaviour has been shown, for example, in the case of myrmecochory (BEATTIE 1991, HUGHES et al. 1994, KAUFMANN 2002). Evidence for chemical signalling between ants and plants in specific ant-plant protection symbioses comes from recent studies by AGRAWAL (1998), AGRAWAL & DUBIN-THALER (1999), and BROUAT et al. (2000). Whereas the first two studies deal with ant response to volatile plant cues associated with herbivory and nestmate recruitment to damaged sites, the latter examines ant patrolling of *undamaged* sites. Although circumstantial evidence indicates that *Cladomyrma* ants indeed respond to host plant injuries (see p. 230), 'neophily' cannot be explained by plant cues related to

herbivory because it occurs on intact healthy new plant tissue. Therefore, the following discussion will focus on the attractiveness of intact, undamaged young plant parts to *Cladomyrma*.

BROUAT et al. (2000) hypothesise that the host plant *Leonardoxa africana* subsp. *africana* encourages young-leaf patrolling of the symbiotic ant *Petalomyrmex phylax* by releasing 'green-leaf volatiles' (e.g., hexenal and hexenyl acetate) and methyl salicylate (a phenolic compound). Although such compounds are reported as common components of numerous plant species belonging to a variety of plant families (BROUAT et al. 2000, and references therein), the authors found a major difference between young leaves of the myrmecophytic *L. a. africana* and the non-myrmecophytic *L. a. gracilicaulis*, i.e., a highly unusual dominance of methyl salicylate in the young-leaf extract of the myrmecophyte.

It is important to note that the differences between the two subspecies of *Leonardoxa* in chemical composition of extracts of young leaves were strictly quantitative. BROUAT et al. (2000) suggest that selection in the context of signalling between ant-plant and plant-ant has acted on leaf chemistry and changed the relative concentrations of pre-existing compounds. Because in mutualistic ant-plant associations the fitness of ants can be tightly linked to plant growth and survival, direct rewards would not be necessary to induce ants to patrol young leaves. Attraction of *Petalomyrmex phylax* ants to methyl salicylate or 'green-leaf volatiles' may thus be the proximate mechanism explaining the restriction of ant patrolling to young leaves. [The authors, however, do not exclude the alternative explanation, i.e., that these substances may serve as a resource for the ants because they are known to possess antiseptic and fungistatic properties.]

Recently, EDWARDS et al. (2007) tested another hypothesis for ‘neophily’ in the neotropical *Cordia-Allomerus* mutualism: new shoots chemically mimic ant brood or alarm pheromones (a ‘sensory trap’) and thereby elicit worker patrolling of vulnerable plant parts. However, patrolling *Allomerus* workers were attracted only to new leaves, whereas brood-tending workers collected from inside plant domatia (‘nurses’) were attracted to *Allomerus* brood rather than to new leaves. Only patrollers were attracted to new leaves significantly more than to mature leaves, and nurse workers were larger than patroller workers, which suggests that the behavioural differences reflect caste differentiation. Therefore, the sensory trap hypothesis was rejected.

8.4.5. What is the cue by which *Cladomyrma* ants can recognise young plant tissue?
This question cannot be answered yet, but that does not stop me from speculating. Testing for cues requires both chemical studies of myrmecophytic host plant species and of their relatives as well as bioassays with associated *Cladomyrma* ants. Nevertheless, a speculative discussion of possible cues may suggest avenues for approaching this unexplored aspect of the chemical ecology of symbiotic ant-plant mutualisms.

A striking result of my study is the occurrence of 'neophily' across all *Cladomyrma* species tested, despite the (in part extreme) taxonomical distance between the associated host plants. It is hard to imagine that each host evolved a particular compound capable of attracting ants to young plant tissue. Furthermore, this hypothesis would require that all host plants of a certain *Cladomyrma* species – for example, *C. petalae* associates with six host species from four plant families – either developed the same (or a closely related) specific attractant compound, or that a diverse set of substances releases ant patrolling in a single *Cladomyrma* species similarly. In contrast, it is much more conceivable that widespread and common substances present in developing tissue of many plant species across families serve as attractants. If true, the stereotyped and continuous patrolling of *Cladomyrma* on young and vulnerable parts of its hosts may then be elicited by differences in the amount of common compounds present in young and mature leaves.

What cues could be at the base of 'neophily' in *Cladomyrma* workers? Analyses of volatile organic compounds by BROUAT et al. (2000) and MAYER, SCHABER & HADACEK (2008) have shown for the *Leonardoxa-Petalomyrmex* and the *Piper-Pheidole* association, respectively, that 'green-leaf volatiles' (such as isomers of hexanal, hexenol, and hexanyl acetate) and methyl salicylate or the sesquiterpene β-caryophyllene are likely candidates. These compounds are known to play diverse roles in interspecific interactions. Phytophagous insects are capable of responding to differences in abundance and composition of 'green-leaf volatiles' between young and mature leaves (LIGHT et al. 1993). Emission of 'green-leaf volatiles' by the plant is often associated with leaf damage and are reported to be attractants for various phytophagous insects and insect predators (TURLINGS, TUMLINSON & LEWIS 1990, AGRAWAL 1998, MÜLLER & HILKER 2000). Methyl salicylate is also commonly emitted by plants, and may attract pollinators or natural enemies of phytophagous insects (DICKE et al. 1990, KNUDSEN & TOLLSTEN 1993, SHULAEV, SILVERMAN & RASKIN 1997, JAMES 2003). A closely related compound, methyl-6-methyl salicylate, appears to play a role in seed dispersal by some ants (DAVIDSON, SEIDEL & EPSTEIN 1990, SEIDEL, EPSTEIN & DAVIDSON 1990). β-Caryophyllene has been shown to cause agonistic

behaviour, which includes repellency, alarm, self-grooming, arrestant behaviour and subsequent fighting in the leaf- cutting ant *Atta sexdens rubropilosa* (NORTH et al. 2000).

Although highly speculative, I assume that recognition of, and attraction to, young plant tissue by *Cladomyrma* (and other plant-ants) is based on a rather universal eliciting cue (such as 'green-leaf volatiles' and methyl salicylate), and that the relative concentrations of these compounds in young and mature leaves may be sufficient to modulate the ant's response. [It's noteworthy, however, that 'green-leaf volatiles' may be absent from some non-myrmecophytic plants, e.g., in *Piper* (MAYER, SCHABER & HADACEK 2008).] Additional support for the hypothesis of a universal cue distinguishing young from older plant parts may come from the pruning behaviour of *Cladomyrma* (chapter 10). Most *Cladomyrma* species tested do not trim off alien plants touching their host indiscriminately. Rather, the ants preferentially cut young developing tissue such as immature leaves or petioles. It remains to be tested, however, if pruning ants recognise young tissue of alien plants via chemical cues (taste or odour) or if they simply respond to the 'hardiness' of the tissue into which they bite. Locally induced responses have been shown to be unspecific in another plant/ant system. *Allomerus* workers recruit nest-mates after discovering extracts not only from their *Hirtella* host, but also from non-host plant species of a different plant family (ROMERO & IZZO, 2004). The lack of specificity in the response of ants suggests that very general cues are used in inducing ant recruitment to *Hirtella*.

8.4.6. Why do *Cladomyrma* species preferentially patrol young plant tissue?

A possible proximate mechanism for explaining the restriction of ant patrolling to young plant tissue has been discussed above. An alternative explanation, however, cannot be excluded. When patrolling young leaves workers of all *Cladomyrma* species often stop for brief periods and appear to survey or lick the leaf thoroughly, although the surface appears intact and clean. The significance of this behaviour is unknown. A similar behaviour is also reported for the plant-ant *Petalomyrmex phylax* (BROUAT et al. 2000). Do the ants collect plant-derived antiseptic or fungistatic compounds? Methyl salicylate and some 'green-leaf volatiles possess such properties (BLUM 1996). Plant-ants nesting in narrow, hollow twigs may be especially prone to attacks by microbial nest pathogens. In a number of ants the metapleural gland secretions serve as antiseptic substances (MASCHWITZ 1974, ATTYGALLE et al. 1989). The metapleural gland of *Cladomyrma* is well developed, but it remains to be tested if antiseptic secretions are produced. Do the specific nesting conditions of plant-ants necessitate the additional application of plant-derived fungistatic compounds? Here again, this

study suggests the interest of examining the chemical ecology of the *Cladomyrma*-plant complex.

The conspicuous behaviour of *Cladomyrma* patrolling and 'licking' young leaves may also be interpreted in the context of biotic defense (for a detailed discussion of the latter see chapter 9). If *Cladomyrma* clean their host from plant pathogens and epiphyllae, or protect it against herbivorous insects, it could well increase photosynthetic rates, leaf longevity or survival (FONSECA 1994, SANTOS 2000). Thus, patrolling of young leaves may be maintained by coevolutionary interaction with the plant, i.e., by conferring to the plant a better protection the fitness of the ant colony is increased in turn. This may be an ultimate factor explaining 'neophily' where no immediate and direct benefit to the *Cladomyrma* colony is apparent.

But there is a direct and immediate benefit to *Cladomyrma*. In each host plant species the production of new leaves is linked to the production of new internodes, that is, ant housing structures. Leaves and internodes are produced in a single flush. All newly produced internodes of a suitable diameter are hollowed out and colonised by *Cladomyrma* workers immediately after reaching (almost) their final length, but usually well before their full lignification. In mutualistic ant/plant systems, where plant-ants stay on their host during the entire colony cycle, nesting space is only available through growth of the host plant. Any harm to these future nest sites will have negative repercussions on ant colony development. Therefore, it should be in the interest of the ant colony to secure the development and maturation of all internodes that serve as future ant domatia.

Would it then not be sufficient to concentrate ant activity to new internodes only? Several reasons appear to speak against it. First, internodes and attached leaves develop from young vegetative buds in tight association (as long as leaves do not expand). Any damage to the new shoot would invariably harm both internodes and leaves. Second, the successful development and function of the new leaves probably facilitate later branch growth. Long-term negative effects of simulated defoliation, shoot pruning and shading of a branch on its growth are common (e.g., LANGSTRÖM et al. 1990, HONKANEN & HAUKIOJA 1994, HENRIKSSON 2001), despite possible short-term compensatory mechanisms (GADD, YOUNG & PALMER 2001). Third, the development (or longevity) of an internode may be directly dependent on the successful maturation of the attached leaf. Although plausible, this hypothesis needs to be tested.

Evidence for *Cladomyrma*'s 'selfish' interest in the young internodes as potential nesting sites (and feeding sites for their trophobiotic scale insects) comes from host

plants where more than one internode is produced in a single flush. For example, the two *Cladomyrma* species, *C. andrei* and *C. hobbyi*, inhabiting the woody climbers *Callerya nieuwenhuisii* and *Spatholobus oblongifolius* respectively, tend to prefer the relatively 'older' parts of a new spurt of growth (Fig. 8-8A, B). Usually, the primary diameter of these 'older' internodes is already sufficiently large to become a domatium, whereas the most apical parts have not yet reached the necessary size to house ants. I speculate that the higher ant activity on the relatively older parts of a new spurt of growth reflects the interest of *Cladomyrma* in the suitability of these internodes as domatia. For *Cladomyrma*, the function of patrolling young plant tissue thus appears to ensure the plant's continued capacity to produce resources, that is, nesting space and feeding substrate for trophobionts.

A recent study of the relationship between *Pheidole minutula* and the Amazonian ant-shrub *Maieta poeppigii* (Melastomataceae) bearing leaf-pouch domatia appears to corroborate this hypothesis. CHRISTIANINI & MACHADO (2004) showed that the presence of ants patrolling the leaves of *M. poeppigii* is influenced by the number of domatia on the plant. Furthermore, the mean number of patrolling *Pheidole* ants decreased from young to mature leaves, and from leaves with domatia to those without domatia. As in Cladomyrma, the ant partners of *Maieta poeppigii* cultivate scale insects inside the domatia and feed on their exudates. The preference of patrolling *Pheidole* ants for young leaves having domatia thus reflects the importance of the leaves as ant domiciles and feeding substrate for the associated scale insects.

9. Protection against herbivory

9.1. INTRODUCTION

In ant-plant interactions ants are incorporated to various degrees into the defence systems of plants against herbivores. Defence via housed or attracted ants is indirect and can be viewed as an *inducible*, *biotic* defence (AGRAWAL & DUBIN-THALER 1999), because of the ants' sensitivity to cues associated with herbivory, their rapid recruiting and fighting abilities, and their reclaimable and redeployable nature as a plant defence. In obligate myrmecophytes (ant-plants), which offer housing and often food for their ant partners, the ants are known or presumed to protect the plants from herbivory (e.g., *Acacia*: JANZEN 1967, PALMER & BRODY 2007; *Barteria*: JANZEN 1972; *Cecropia*: SCHUPP 1986, AGRAWAL 1998; *Endospermum*: LETOURNEAU, ARIAS & JEBB 1993; *Leonardoxa*: GAUME, MCKEY & ANSTETT 1997, GAUME & MCKEY 1998; *Macaranga*: FIALA et al. 1989 and 1994a, FEDERLE, MASCHWITZ & FIALA 1998b, ITIOKA et al. 2000, HEIL et al. 2001a; *Maieta*: VASCONCELOS 1991, LAPOLA, BRUNA & VASCONCELOS 2003; *Piper*: RISCH 1982, LETOURNEAU 1998; *Tachigali*: FONSECA 1994; *Tetrathylacium*: SCHMIDT & MAYER 2000; *Tococa*: ALVAREZ et al. 2001, BIZERRIL & VIEIRA 2002, BRUNA, LAPOLA & VASCONCELOS 2004).

This body of work has demonstrated that ants often defend plants and have the potential to increase plant fitness. Benefits to the plant may also include increased leaf longevity or leaf number, protection against pathogenic fungi, allelopathy (removal of vines and/or clearing of the area around the base of the host), nutrient addition through breakdown of food remains and collected debris in domiciles, and absorption of ant-respired carbon dioxide (e.g., JANZEN 1969 and 1972, CAMPBELL, RICHARDSON & ROSAS 1989, MORAWETZ, HENZL & WALLNÖFER 1992, MASCHWITZ & FIALA 1995, TRESEDER, DAVIDSON & EHLERINGER 1995, LETOURNEAU 1998, SUAREZ, DE MORAES & IPPOLITO 1998, HEIL, STAEHELIN & MCKEY 2000, SAGERS et al. 2000, SANTOS 2002, FEDERLE, MASCHWITZ & HÖLLDOBLER 2002, OLESEN et al. 2002, FISCHER et al. 2003).

The aim of this study was to use experimental manipulations in the field to investigate whether *Cladomyrma* ants, one of the most abundant plant-ants in SE Asia, are involved in a protective mutualistic system. More specifically, I asked: (1) How do *Cladomyrma* ants react when encountering a herbivorous insect on their host plant? (2) Do *Cladomyrma* ants have an effect on the amount of plant photosynthetic surface lost to herbivores, i.e., on herbivore damage of young developing leaves?

Many studies have shown that a protective effect is not restricted to mutualistic associations involving specific, obligate ant partners, but that opportunistic ants visiting extrafloral nectaries can also provide a significant reduction in leaf herbivory (e.g., BENTLEY 1977a and 1977b, KOPTUR 1984, FARJI-BRENER, FOLGARAIT & PROTOMASTRO 1992, FIALA et al. 1994a, DEL-CLARO, BERTO & REU 1996, FUENTE & MARQUIS 1999, OLIVEIRA et al. 1999, HEIL et al. 2001a and 2001c). Nevertheless, benefits conferred by ants to plants vary strongly among systems and are not always clear (HEIL et al. 2004a, GAUME et al. 2005, FREDERICKSON & GORDON 2007). This variability in interaction can have both a temporal and spatial component (BARTON 1986, BRONSTEIN 1994, ALONSO 1998, RICO-GRAY et al. 1998, HOSSAERT-MCKEY et al. 2001, MOOG, FELDHAAR & MASCHWITZ 2002).

Associations in which the partners form close relationships, such as myrmecophytes harbouring specific plant-ants, are, however, known or presumed to be better protected by their ant partners than plants visited or colonised by facultative ant species (DAVIDSON & MCKEY 1993a, FIALA et al. 1994a, VASCONCELOS & DAVIDSON 2000, HEIL et al. 2001a, LINSENMAIR et al. 2001).

The tree *Saraca thaipingensis*, a common host plant of *Cladomyrma petalae*, is occupied in part by an opportunistic *Crematogaster* ant species. This provides an interesting opportunity to test if the hypothesis of a higher protective efficacy of symbiotic plant-ants (*Cladomyrma*) compared to facultative ants (*Crematogaster*) can be supported.

9.2. MATERIALS AND METHODS

Study sites

The field investigations were carried out (i) on the Malay Peninsula in the Ulu Gombak Valley (*Crypteronia*, *Saraca*) and the Genting Highlands (*Spatholobus*), and (ii) on Borneo at Poring Hot Springs, Sabah (*Callerya*, *Drypetes*, *Neonauclea*). Information about the sites is provided in MEDWAY (1972) and DAVIS, HEYWOOD & HAMILTON (1995).

Ant response to herbivorous insect larvae

I collected living lepidopteran larvae of small to medium size (4-40 mm) from host and non-host plant species. They were then delicately placed on immature leaves of inhabited twigs to prevent alarm recruitment of the ants. In order to standardise measurements on ant activity, I recorded the number of ants on the young foliage at least 2 minutes prior to the experiment and only started the trial when exactly one ant worker was present. Then, the number of ants on the leaf was recorded in subsequent 30-second intervals for 20 minutes, and the behaviour of the ants and the fate of the caterpillars were noted. Particularly, I measured the time spent (i) before the larva was found, (ii) attacked, or (iii) repelled/killed by the workers.

Taxa tested:

- *Cladomyrma andrei* (on *Callerya nieuwenhuisii*): Hesperiidae (probably *Hasora* sp.), n=2; Limacodidae, n=3; Lycaenidae (*Anthene* sp.), n=1; total n=6.
- *Cladomyrma maschwitzi* (on *Crypteronia griffithii*): Limacodidae, n=2; Lycaenidae (*Jamides pura*), n=2; Noctuidae (Sarrothripinae), n=3; and undetermined Lepidoptera, n=3; total n=10.
- *Cladomyrma petalae* (on *Saraca thaipingensis*): Geometridae, n=2; Limacodidae (1x *Thosea* sp.), n=3; Lycaenidae (*Anthene emolus*, 2x *Jamides pura*, *Drupadia theda*), n=4; Lymantriidae, n=1; Noctuidae (Sarrothripinae), n=4; Notodontidae, n=1; Satyridae, n=1; total n=16.
- *Cladomyrma yongi* (on *Drypetes longifolia*): Geometridae, n=1; Limacodidae, n=2; Lycaenidae, n=2; and undetermined Lepidoptera, n=3; total: n=8.

Each larva was tested at a different *Cladomyrma* colony or, in the case of *C. petalae* on *Saraca* where six of the 16 tests were conducted on the same colony, at least one day elapsed between the trials (by which time the observation of the ant's behaviour was independent from the previous observation). All 40 trials were conducted during mid-day to afternoon (12.00–16.00 h), when activity levels of *Cladomyrma* workers are usually highest. In all cases, colony size was estimated to exceed 400 workers. To test whether the ant number increased on young foliage as a response to the experimentally placed larvae encountered by the workers, I compared for each trial the pre-experimental activity level (mean of 2 minutes; 5 counts) with the post-detection level (mean of 2 minutes after detection; 5 counts) by using the non-parametric Wilcoxon test for matched pairs.

Ant response to insect eggs

Groups of ten termite eggs were cautiously placed onto the base of young apical leaves of both *Crypteronia griffithii* (n=10) and *Saraca thaipingensis* (n=8) inhabited by *Cladomyrma maschwitzi* and *C. petalae*, respectively. Next, I recorded worker behaviour for one hour continuously; if termite eggs were still present after one hour, I checked their number in subsequent 1-hour intervals. Trials were conducted during daytime between 11.00 and 15.00 h. Colony size varied, estimated to exceed 500 workers in most cases (n=16), but probably less than 200 in two trials.

Ant protection of young leaves

To determine whether *Cladomyrma* workers protect young leaves of their host plants from herbivory, I compared herbivore damage of young leaves with natural ant fauna with that of leaves from which ants had been experimentally excluded (Tab. 9-1). From each of five different host plant taxa I located 10 to 14 plants occupied by *Cladomyrma*, each of which bore at least two twigs with intact young leaves of similar initial size (not longer than 10 cm). One young apical leaf was haphazardly chosen as control; this unmanipulated leaf was patrolled by workers of the resident colony. Any ants present were removed from the other leaf (experimental), and the hollow interior of the twig was plugged with ca. 1 ml of glue pressed inside through the most apical entrance hole. Then, both the apex of the twig and the base of the leaf petioles were coated with a sticky resin (Tangle-Trap, Tanglefoot Corp., Grand Rapids, Mich., USA) in order to prevent ants from other nest parts to forage or patrol on the experimental twig.

> For *Crypteronia* only: A small amount of a neurotoxic pyrethroid insecticide (Spruzit, Neudorff, Emmerthal, Germany; 1% solution) was injected through the most apical entrance hole with a syringe. After five minutes, the liquid was blown out through the entrance holes to prevent any detrimental effect of Spruzit on the plants. During the course of the experiments, however, I came to the conclusion that this procedure is not necessary, because tangle-trap –if amply applied and checked regularly for integrity– is a sufficient means to exclude the ants from the experimental leaves.

This paired design reduces the effect of natural variation between trees and colonies, therefore the results are not biased by site or genetic differences between experimental plants. The plants were controlled in intervals of one (*Saraca*, *Neonauclea*) or three days (*Crypteronia*, *Drypetes*, *Spatholobus*) to verify that experimental leaves were devoid of patrolling ants. The experiments continued until the leaves reached maturity. Maturity was defined as the point when leaves reached full size and became completely green, erect and tough (about 20–45 days). Paired

leaves were always harvested at the same time to ensure that temporal exposition to herbivory did not differ between experimental and control leaves.

Table 9-1: Treatment groups of experiments on young leaf herbivory. Asterisk (*): the original experimental design included 10 Bornean *Drypetes* trees with a total of 18 leaf pairs. Unfortunately, the experimental setups at five plants were destroyed before the end of the experiment. Thus only eight leaf pairs could be used for data analysis.

taxa host plant - ant	*n* trees	*n* leaf pairs	category
Crypteronia griffithii - Cladomyrma maschwitzi	10	20	inhabited vs ant-free
**Drypetes longifolia - Cladomyrma yongi*	5	8	inhabited vs ant-free
Neonauclea gigantea - Cladomyrma dianeae	11	18	inhabited vs ant-free
Spatholobus bracteolatus - Cladomyrma petalae	12	20	inhabited vs ant-free
Saraca thaipingensis - Cladomyrma petalae	14	33	inhabited vs ant-free
Saraca thaipingensis - Crematogaster sp. 1	11	20	inhabited vs uninhabited (free access to EFN)

Variation of the experimental design

A part of the *Saraca* population in the Gombak valley was inhabited by a *Crematogaster* species, *C.* sp. 1, which nested facultatively in hollowed-out twigs. Usually only a fraction of the available twigs were occupied by *Crematogaster*, and other twigs of the same individual tree were free of nesting ants (see chapter 4, p. 53). Thus, young developing leaves were selected from inhabited (controls) and uninhabited (experimentals) twigs. However, I did not apply tangle-trap to the experimental twigs and leaves, because I wanted to allow ants (such as tourist ants from neighbouring plants as well as *Crematogaster* sp. 1 from the host tree) to visit the extrafloral nectaries (EFN) which are active on young *Saraca* leaflets. This paired design compares leaf damage of twigs inhabited by *Crematogaster* sp. 1 with that of unoccupied twigs that are accessible to ant visitors exploiting the EFN.

Measuring herbivory

After maturation, the leaves were collected and dried to measure the plants' remaining intact leaf area and to reconstruct the original entire surface. Leaf damage of *Saraca* and *Crypteronia* was measured for each leaf using a Leaf Area Meter (Mod. LI-3100, LI-COR, Lincoln, Nebr., USA) and was expressed as a percentage of the missing leaf area. A different method of measuring leaf damage was applied for *Drypetes, Neonauclea*, and *Spatholobus*: digitized images of leaves were captured and analysed using NIH Image (developed at the U.S. National Institutes of Health and available on the Internet at *http://rsb.info.nih.gov/nih-image/)*. For heavily damaged leaves (for

which a reconstruction of the original leaf margin was not possible), the area of a single leaf was estimated by measuring length or width and using equations obtained by regressions of randomly collected, intact leaves (for each plant taxa $r^2 > 0.96$). If a leaf (*Crypteronia*, *Drypetes*, *Neonauclea*) or leaflet (*Saraca*, *Spatholobus*) had been almost entirely eaten, its area was estimated by measuring the companion leaf/leaflet.

Data analysis

Data on leaf area losses were, in general, not normally distributed. In addition to a high number of small values, a small number of high values up to 100% occurred. For this reason, nonparametric statistics were used. The statistical analysis of the pairwise experimental arrangement was conducted with the Wilcoxon signed-ranks test for matched pairs (zero differences dropped, two-tailed). For analysis of non-paired experiments (e.g., herbivory of *Cladomyrma*- versus *Crematogaster*-inhabited *Saraca* trees) the non-parametric Mann-Whitney U-test was used. All statistical evaluations were conducted with StatView 4.51 for Macintosh (Abacus Concepts, Inc., Berkeley, California, USA).

9.3. RESULTS

9.3.1. Ant response to insect herbivores

The results of the 40 trials in which lepidopteran larvae were placed on young immature leaves are summarised in table 9-2 (see below). Only in two trials the *Cladomyrma* ants were not successful in discovering the caterpillar within the 20-min period (note that exactly one ant was present on the leaf at the start of each trial). In four trials an ant detected the larva but nevertheless 'ignored' the intruder and continued patrolling the leaf – the causes of this behaviour are unknown. In two of these cases the ant even appeared to keep some distance when passing the caterpillar. In all the remaining trials (n=34) the ants had at least a temporal repellent effect on the introduced larvae.

The fate of the larvae was subject to a considerable degree of variation: (i) they escaped to adjacent mature leaves where ants did not follow, or (ii) fell off the young leaf but remained attached by a silk thread (these larvae may be able to return to attack the young leaf again); (iii) the larvae fell to the ground, either by ants throwing them off the leaf or, apparently, by deliberately losing hold to avoid further attacks by the ants (sometimes carrying along an ant bitten into the larva); and (iv) the larvae were killed by the ants and thrown off the leaf. In the latter cases (n=6), I never observed the ants feeding on the killed caterpillars.

Table 9-2: Fate of lepidopteran larvae placed on young foliage (n=40). [For explanation of category "ignored" refer to text.]

fate of larva	*n*	%	effect	%
not located	2	5		
"ignored"	4	10	unsuccessful:	15
repelled: hiding among leaflets	1	2.5		
repelled: escape to mature leaf	7	17.5		
repelled: escape on silk thread	5	12.5	temporal:	32.5
repelled: fell to ground	15	37.5		
killed: thrown off the plant	6	15	permanent:	52.5

To summarise, in 85% of the trials the ants had a temporal or permanent effect on the caterpillars placed on young leaves. On average the number of ants on the young leaf increased after discovery of the larvae (Fig. 9-1, pooled data).

This increase in ant activity is due to recruitment of nestmates. Often, the *Cladomyrma* worker which found the larva soon returned to the nearest entrance hole in the adjacent internode. Several seconds or a few minutes later a group of ants emerged that directly headed for the affected leaf and jointly attacked the caterpillar. The increase of the mean number of ants for three 2-min intervals during the experiment is shown in figure 9-2. A statistical comparison of the pre-experimental ant activity level ("before start") and ant activity level after discovery of the larva ("after detection") is highly significant (P <0.0001, z = 5.114, Wilcoxon test for matched pairs; n=38, two cases omitted due to missing values).

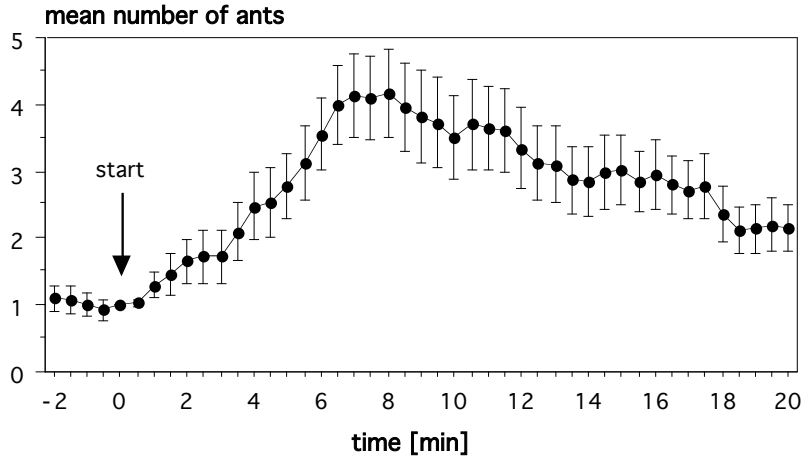


Figure 9-1: Mean number of *Cladomyrma* ants after placing lepidopteran larvae on young leaves. Data of all 40 trials pooled. *Error bars* = standard error (± SE). *Arrow* = indicates start of the experiment; included are two minutes of pre-experimental ant activity (-2 to 0 min).

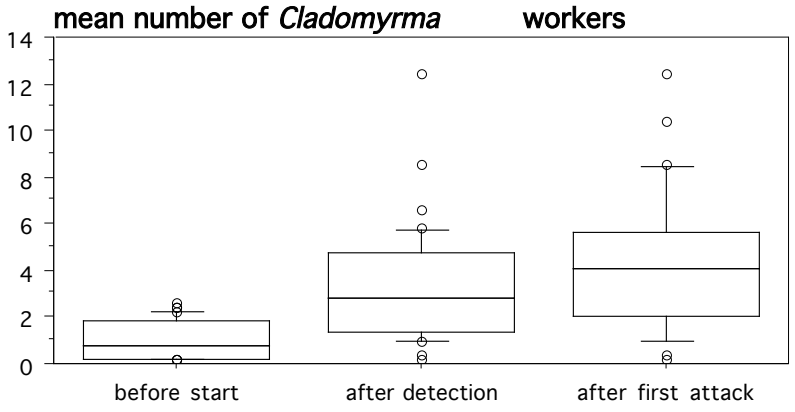


Figure 9-2: Box-whisker plots of the mean number of ants within a 2-min interval (5 counts) for three categories: "before start" = pre-experimental ant activity level (-2 to 0 min), "after detection" = activity level after discovery of the larva, and "after first attack" = activity level after the first bite into the larva; n = 40 trials. [For explanation of box-whisker plots see fig. 4-45.]

The mean time for the first worker to discover the caterpillar was 5 min 47 s (considering only trials in which the larva was found within the 20-min period). However, detection time varied strongly from 12 s to 15 min 42 s (median 4 min 10 s). Time of first attack (mean 5 min 52 s) differed only slightly from detection time (Fig. 9-3) because the ant who found the larva usually attacked the caterpillar immediately or shortly after discovery. Whether the ant that found the larva recruited nestmates or attacked the larva independently, the fate of the larva was predictable. After an average of 8 min 5 s (median 6 min 54 s) the caterpillar was temporarily or permanently removed from the young foliage (Fig. 9-3).

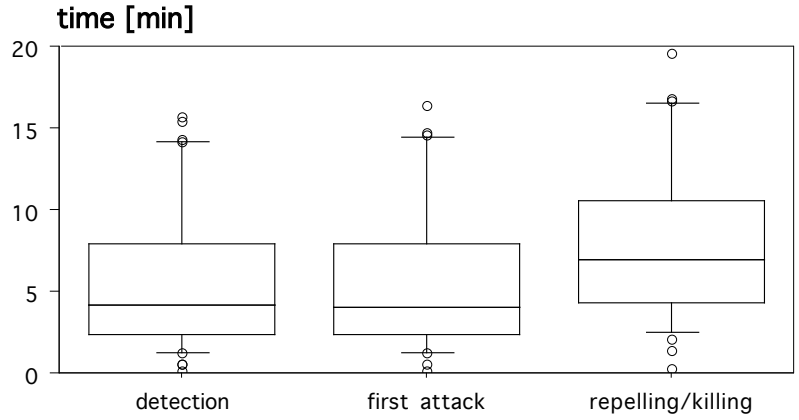


Figure 9-3: Box-Whisker plots of the time *Cladomyrma* ants needed to discover, attack or repel/kill the lepidopteran larvae placed experimentally on young leaves (based on 40 trials). [For explanation of box-whisker plots see figure 4-45.]

The *Cladomyrma* ants displayed a stereotyped behaviour towards the caterpillars irrespective of the ant species studied. When encountering a larva, workers of each of the four species – *C. andrei*, *C. maschwitzi*, *C. petalae*, and *C. yongi* – raised their gaster and inspected the alien object closely. This often resulted in an immediate attack (bite) or in the recruitment of nestmates (Fig. 9-4A, D). During that time the ants were in an excited state and distinctly increased their speed. If a caterpillar tried to escape, the ants followed close behind and continued their attacks. Only when the intruder reached older adjacent plant parts, the ants' effort to follow decreased and, eventually, the larva could rest on mature leaves. This outcome of an encounter between *Cladomyrma* and caterpillar was mostly seen in trials where bigger-sized caterpillars (20-–40 mm long) were used.

Figure 9-4 (next page): Examples of the experiment in which lepidopteran larvae were placed on young leaves of plants inhabited by four *Cladomyrma* species. *d* = detection of larva; *a* = first attack on the larva; *e* = escape of larva, either by moving to an adjacent mature leaf (A) or by hanging on a silk thread from the leaf (B); *f* = larva fell to ground after being attacked (C); and *k* = larva killed and thrown off the leaf (D). Examples are selected to show the observed variations of ant activity and ant behaviour in response to introduced caterpillars. [Note that the differences are not attributable to the ant species; each ant species can show each of the patterns selected.]

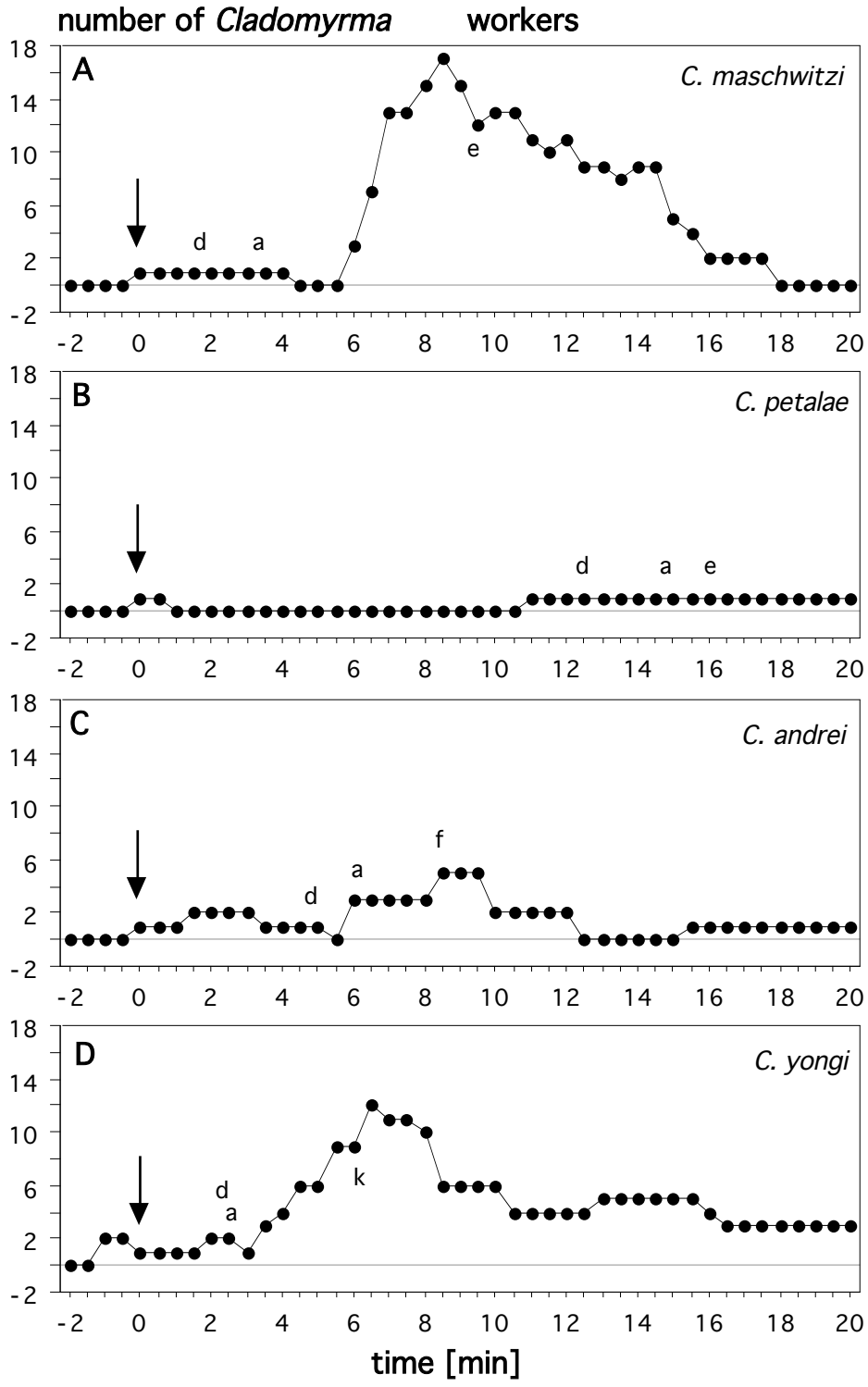


Figure 9-4

Some exceptions in the response of the ants to lepidopteran larvae on young foliage are noteworthy. As previously stated, ants sometimes 'ignored' the caterpillars. These

cases involved two noctuid and two limacodid larvae. In the latter two, the ants appeared to even avoid the contact with the caterpillars, perhaps because the larvae of this lepidopteran family possess stinging hairs (in seven other tests involving limacodids the ants successfully repelled the larvae despite their arming). Another source of variation in the response of *Cladomyrma* ants to herbivorous insect larvae is the number of ants involved to force caterpillars off the young foliage. Recruitment of nestmates may increase the number of ants considerably (Fig.9-4A, D), and after subsequent repellence or killing of the larva, ant activity decreased slowly, usually reaching the pre-experimental level only after several minutes (Fig. 9-4A, C). However, a single ant worker may be sufficient to cause the departure of the caterpillar from an immature leaf (Fig. 9-4B). Thus, recruitment after detection of an herbivorous larva is a commonly but not obligately released behaviour in *Cladomyrma* ants.

Variation in both the behavioural response of the ants to caterpillars and the outcome of these interactions may strongly be influenced by the species-specific defensive traits of the caterpillar encountered. Apart from the fact that bigger-sized larvae generally appear to have a better chance to escape to adjacent plant parts (see above) some caterpillar species possess the ability to escape –at least temporarily– from an attack by lowering themselves on a silk thread, thus getting out of reach of the *Cladomyrma* ants. The long-term effect of this trait, however, was not tested in my experiments, and thus the relevance of such defensive traits with regard to the fate of the larvae is subject to speculation.

Certain immature lycaenid taxa form non-aggressive associations with ants (MASCHWITZ & FIEDLER 1988). These so-called 'myrmecophiles' are able to break the ants' communication code and to suppress ant aggressiveness, e.g., by secretion of appeasement substances. My experiments included some of these myrmecophilous taxa (*Anthene emolus*, *Drupadia theda*, and *Jamides pura*) and the outcomes of the encounters with *Cladomyrma* are intriguing. In all trials (n=9) the larvae were killed (56%) or removed from the plant surface (44%). In the latter cases the attacked caterpillars fell to the ground before being killed, but it was not always clear if they were thrown off the leaf by the ants or lost hold. The result, however, was a permanent departure of the myrmecophilous lycaenid larvae from the young leaves in each of the *Cladomyrma* species tested (Fig. 9-5).

Figure 9-5: Lepidopteran larvae on young leaves of *Saraca thaipingensis*. **A**: the myrmecophile *Anthene emolus* (Lycaenidae), associated with the weaver ant *Oecophylla smaragdina*, causes severe damage on young foliage; **B**: the myrmecophile lycaenid *Drupadia* is being attacked by workers of *Cladomyrma petalae*; **C**: a limacodid caterpillar suffers from an attack by *C. petalae*; and **D**: recruited workers of *C. petalae* attack the myrmecophile *Anthene emolus* (D: courtesy of Peter Seufert).

9.3.2. Field observations of unprovoked encounters with insect herbivores

Attacks of *Cladomyrma* workers against insect herbivores naturally present on host plants have been observed occasionally. For instance, both *C. petalae* and *C. maschwitzi* were observed to attack case moth larvae (Psychidae, Lepidoptera) on

young internodes (Fig. 9-6). Up to eight workers tried to remove the larvae but the workers were unable to lift the protecting case. Nevertheless, the workers always succeeded in driving off the invaders to adjacent old plant parts, then ceased their hostility and returned to patrolling the young foliage.

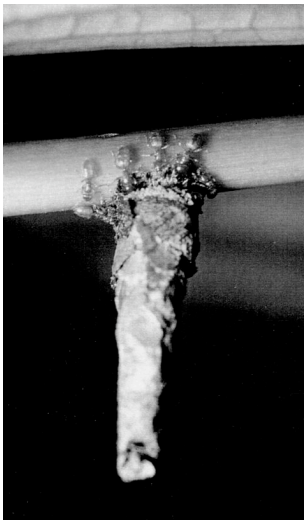


Figure 9-6: *Cladomyrma maschwitzi* workers attacking a psychid case moth larva on a young internode of *Crypteronia griffithii*.

Adult chrysomelid beetles of the genus *Theopea* (Galerucinae; det. M. Schöller) are commonly found on the foliage of *Saraca thaipingensis* in the Gombak valley, Peninsular Malaysia. Although it is not known if these beetles feed on the leaves, I noticed twice that approaching *C. petalae* ants caused *Theopea* to fly off the leaf. A similar deterring effect of the *Cladomyrma* ants was observed towards several Auchenorrhyncha taxa that commonly suck on young shoots of unoccupied *Saraca* trees. When cicadellids or cercopids recognised the proximity of *C. petalae* ants they abandoned their feeding site and flew off (n=14). Apparently, *C. petalae* ants also discouraged female lycaenid from egg-laying. Females observed to search for an oviposition site avoided *Cladomyrma*-inhabited *Saraca* trees and directed their search to neighbouring *Saraca* trees (P. Seufert, pers. comm., and own obs.).

These observations are supported by indirect evidence, i.e., *Saraca* trees occupied by a mature *Cladomyrma* colony were usually free of lycaenid and other lepidopteran egg patches. However, the lack of lepidopteran egg patches may also be explained by the 'cleaning behaviour' of *Cladomyrma* ants.

9.3.3. Ant response to insect eggs (cleaning behaviour)

Batches of ten termite eggs had been placed on the base of young leaves of both *Crypteronia griffithii* and *Saraca thaipingensis*. The pooled data are presented below (Fig. 9-7).

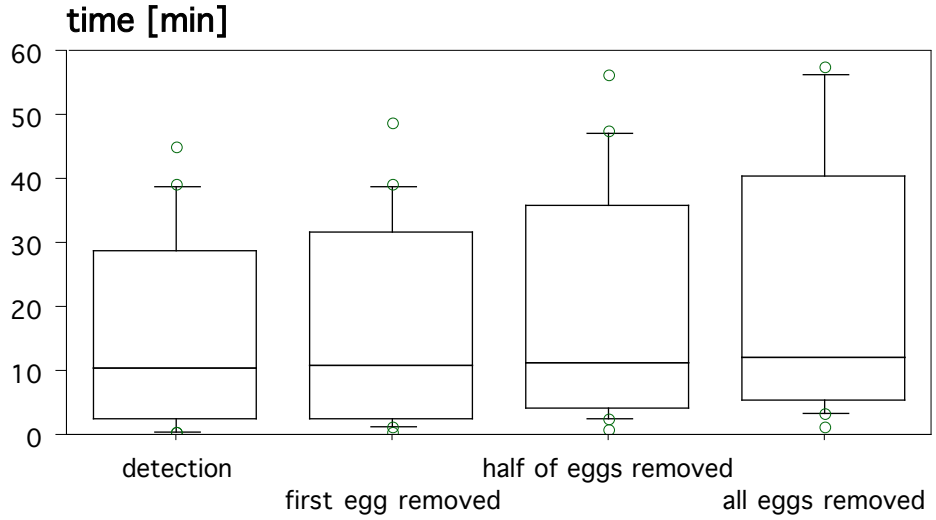


Figure 9-7: Box-Whisker plots of ant response to termite eggs placed on young leaves of *Crypteronia griffithii* and *Saraca thaipingensis*, inhabited by *Cladomyrma maschwitzi* and *C. petalae*, respectively. Given is the time needed for *Cladomyrma* ants to detect and remove the eggs. Data for both species pooled. Included are only those trials in which the eggs were discovered by the ants within one hour (n=16). For more clarity, one outlier (120 min) for column "all eggs removed" has been omitted.

In 16 of the 18 trials conducted the ants discovered the termite eggs within the first hour after start of the experiment. If only these 16 trials are considered the mean time for the first worker to discover the termite eggs was 15 min 22 s and the first egg was removed shortly after discovery (mean 16 min 30 s). On average, all ten eggs were thrown off the leaf surface after 25 min 7 s. The median values (see centre lines of box plots in Fig. 9-7) show that the process of detection of the eggs and their total removal often took less than two minutes. In two trials, however, the ants discovered the termite eggs sometime between the 1st and 2nd and between the 23rd and 24th hour (hourly checks). Although discovery of the eggs was considerably delayed, the ants nevertheless had discarded all eggs successfully by the 3rd and 24th hour, respectively. In both cases the colonies were exceptionally small, probably consisting of less than 200 workers. This may account for the comparatively slow response of the ants to the termite eggs.

The behaviour to remove termite eggs from the leaf surface may be termed 'cleaning behaviour'. Many plant-ants are known to keep the surface of their host plant clean.

When *Cladomyrma* ants encountered small particles such as leaf or pith pieces on the host surface the workers seized these objects with their mandibles, carried them to the stem or leaf margin and let them fall down (Fig. 9-8). Recruitment of nestmates was not observed. As mentioned above the ants also displayed a conspicuous stereotyped behaviour on young, apparently clean leaves. Whether ants regularly remove tiny propagules of fungi or mosses and lichens has not been investigated.

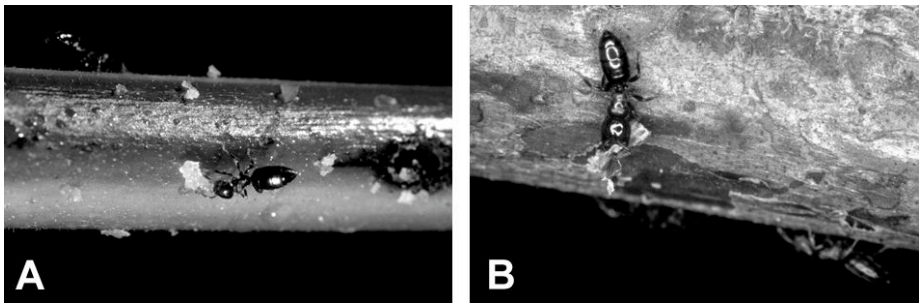


Figure 9-8: Cleaning behaviour of *Cladomyrma petalae* on *Saraca thaipingensis*.
A: a worker seizes a piece of pith; **B**: a worker throws off a bark particle.

9.3.4. Ant protection of young leaves

Chewing insects decrease the photosynthetic surface by removing large portions of the developing leaves. Experimental leaves of all host plants tested accumulated significantly more damage than control (*Cladomyrma*-patrolled) leaves [summarised in Fig. 9-9 and Tab. 9-4]. The mean proportion of leaf area removed by chewing insects was 2.6 (*Spatholobus*) to 7.9 (*Crypteronia*) times greater for experimental leaves (7.1% to 34.1%) than for control, ant-patrolled leaves (1.5% to 8.9%), indicating that chewing insects are important herbivores of young *Cladomyrma* host plant leaves. Thus, the patrolling activity of *Cladomyrma* ants provides very effective protection.

Variations in the mean rates of folivory among host plants and associated *Cladomyrma* species are relatively strong, even on a short-term basis. For example, the host plants of *Cladomyrma petalae*, the tree *Saraca* and the liana *Spatholobus*, showed a mean loss of young leaf area of 8.9% and 6.5%, respectively, whereas *Crypteronia*, inhabited by *Cladomyrma maschwitzi*, had a mean folivory rate of 1.5%. But despite this seemingly stronger protective effect of *Cladomyrma maschwitzi*, the statistical significance levels are higher in *Cladomyrma petalae*, because herbivore damage of experimental leaves (ants excluded) was greater (34.1% and 16.7% in *Saraca* and *Spatholobus*, resp., versus 11.9% in *Crypteronia*).

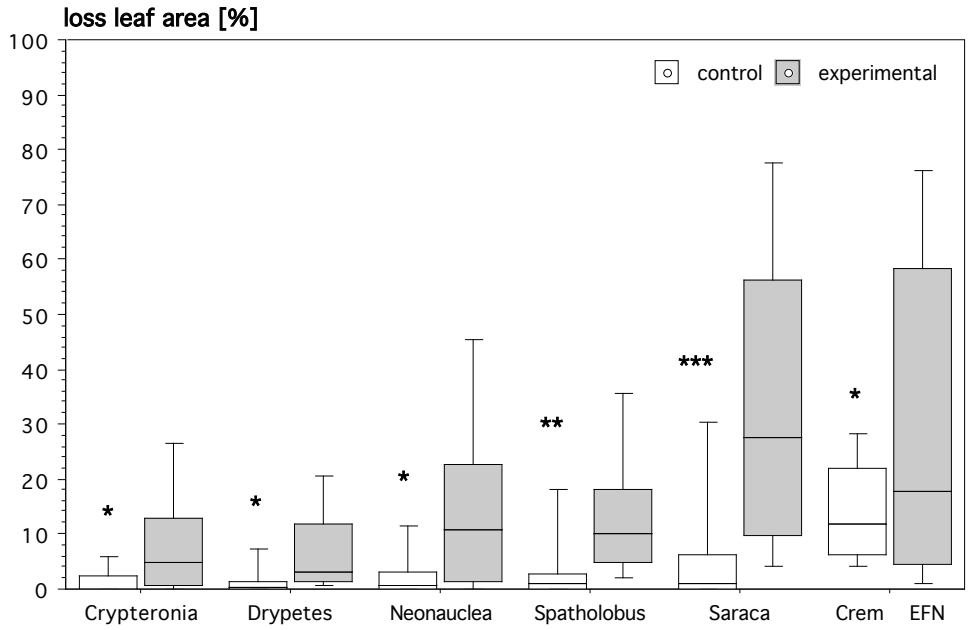


Figure 9-9: Short-term effect of ant exclusion (over 20 to 45 days) on young leaf herbivory of host plants inhabited by obligate *Cladomyrma* ants. Included are also data from *Saraca thaipingensis* (last column) both inhabited by facultative *Crematogaster* ants (Crem) and uninhabited but with free ant access to extrafloral nectaries (EFN). *Asterisks* indicate significant differences within a host plant between experimental leaves (ants excluded) and control leaves (*Cladomyrma* ants maintained) and between Crem and EFN. [For explanation of box-whisker plots see figure 4-45.]

The medians of control leaves (0.0% to 1.0%), however, both differed only marginally between ant species and were distinctly lower than the means, showing that extremes produced a bias (Fig. 9-9, Tab. 9-4). This may point (i) to differences or fluctuations in herbivore pressure among host plant species, or (ii) to a spatial or temporal relaxation of the *Cladomyrma's* patrolling activity (at least in some of the *Cladomyrma* colonies tested), or (iii) to herbivores that either circumvent the ants' guarding behaviour or are not affected by it. In addition, exposure to herbivores differed within and between host plant species due to leaf maturation time (20 to 45 days). Thus, a direct comparison of the protection intensity between *Cladomyrma* species cannot be performed with the short-term experimental design used in this study.

Table 9-4: Short-term effect of ant exclusion (over 20 to 45 days) on young leaf herbivory of host plants inhabited by obligate *Cladomyrma* or facultative *Crematogaster* ants. Included are also data from *Saraca thaipingensis* without ant inhabitants but free ant access to extrafloral nectaries (EFN). Significant differences between control and experimental leaves are given in bold (P<0.05, Wilcoxon test for matched pairs). For analysis of non-paired experiments, the Mann-Whitney U-test was used (indicated by asterisks).

category	*n* leaves	leaf damage [%]: median (mean ± SD)	vs *Crematogaster*	vs EFN access	vs ant-free
Crypteronia griffithii:					
with *Cladomyrma maschwitzi*	20	0.0 (1.5 ± 2.5)			*z* = 2.435 **P = 0.0149**
ants excluded	20	4.8 (11.9 ± 22.5)			
Drypetes longifolia:					
with *Cladomyrma yongi*	8	0.2 (1.6 ± 3.3)			*z* = 1.960 **P = 0.0499**
ants excluded	8	3.0 (7.1 ± 8.1)			
Neonauclea gigantea:					
with *Cladomyrma dianeae*	18	0.6 (5.0 ± 13.1)			*z* = 2.391 **P = 0.0168**
ants excluded	18	10.8 (16.5 ± 19.8)			
Spatholobus bracteolatus:					
with *Cladomyrma petalae*	20	1.0 (6.5 ± 17.3)			*z* = 2.757 **P = 0.0058**
ants excluded	20	10.3 (16.7 ± 21.4)			
Saraca thaipingensis:					
with *Cladomyrma petalae*	33	1.0 (8.9 ± 18.7)	*z* = 3.646 *** P = 0.0003**	*z* = 3.503 *** P = 0.0005**	*z* = 3.852 **P < 0.0001**
with *Crematogaster*	20	11.8 (14.8 ± 10.8)		*z* = 2.278 **P = 0.0227**	*z* = 2.175 *** P = 0.0297**
uninhabited (access to EFN)	20	18.0 (31.8 ± 30.5)			*z* = 0.486 * *P* = 0.63
ants excluded	33	27.5 (34.1 ± 29.0)			

The young leaves of *Saraca* trees harbouring the facultative *Crematogaster* sp. 1 ants suffered, on average, a leaf-area loss of 14.8% (median 11.8%), while plants occupied by *Cladomyrma* lost significantly less of the young leaf tissue (mean 8.9%, median 1.0%; $P = 0.003$, Mann-Whitney). An effect of *Crematogaster* ants on folivory was also visible when compared with uninhabited *Saraca* twigs whose leaves were free to visiting ants exploiting the extrafloral nectaries ($P = 0.0227$, Wilcoxon). A statistical comparison between 'ant-excluded' leaves and leaves of 'uninhabited' *Saraca* plants, however, was not significant ($P = 0.63$, Mann-Whitney).

Mature leaves have not been tested for a protective effect of *Cladomyrma*, because (i) patrolling activity of *Cladomyrma* is confined to young leaves, and (ii) mature leaves appeared to be markedly less affected by herbivory. Those leaves which had been mature at the beginning of the experiments did not suffer (or rarely suffered) any additional loss of leaf area neither on experimental nor control twigs. However, mature leaves can be prone to some degree of herbivore damage. This is especially pronounced in mature leaves of the woody climber *Spatholobus bracteolatus*. In one locality, the Genting Highlands, *S. bracteolatus* was found to be regularly attacked by an unknown, probably flying and nocturnal, insect herbivore that caused small spots of external leaf damage (termed "window-feeding") on mature leaves after *Cladomyrma* ceased to patrol them (Fig. 9-10).

In the Ulu Gombak valley about 5% of all *Crypteronia griffithii* plants colonised by *Cladomyrma maschwitzi* showed a conspicuous damage pattern on some of their mature leaves. The rachis was partly hollowed out and perforated by a series of small holes causing the lamina to twist slightly. In all dissected damaged mature leaves (n=10) the rachis feeding chamber had already been abandoned, indicating that infestation usually takes place during the immature stages of the leaves. The cause was found to be a lepidopteran shoot borer larva chewing through the leaf rachis. A similar series of small holes along the leaf rachis was also produced by an egg-laying, unidentified female cicad. Three weeks later a group of cicad nymphs emerged. Unfortunately, I did not succeed in rearing the caterpillar and the nymphs to maturity.

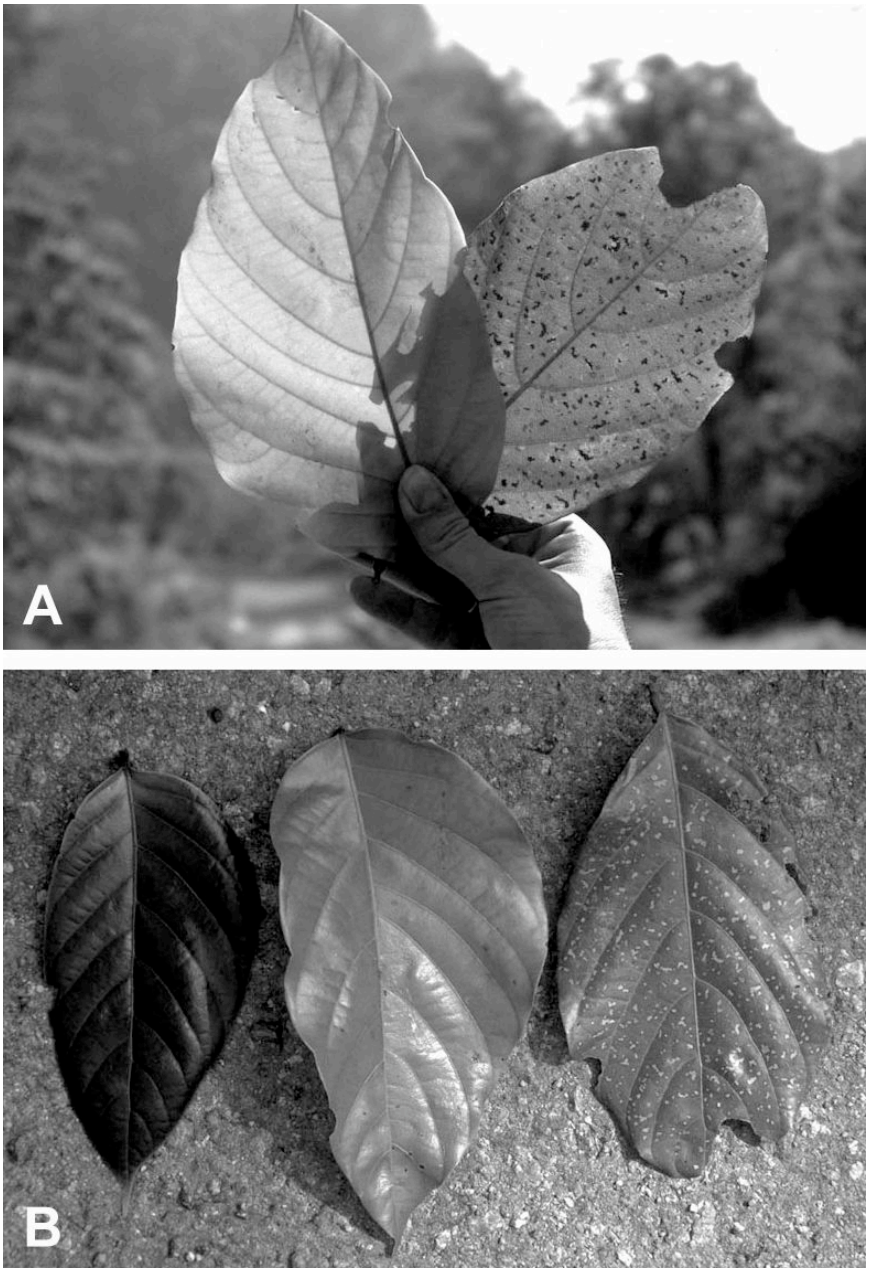


Figure 9-10: Folivory on *Spatholobus bracteolatus* in the Genting Highlands, Peninsular Malaysia. **A**: young, almost matured leaflet without damage (left), mature leaflet with spots of "window feeding" (one epidermis of the leaf eaten); **B**: very young, reddish leaflet and young, almost matured leaflet without herbivory damage (left, middle), and mature leaflet damaged (right).

9.3.5. Summary of the results: protection against herbivory

- workers of all *Cladomyrma* species studied (*andrei*, *maschwitzi*, *petalae*, *yongi*) usually recruited nestmates after detection of caterpillars experimentally placed onto young leaves
- in most cases, caterpillars were attacked by the ants, leading to a temporal or permanent removal of the lepidopteran larvae from young leaves
- *Cladomyrma* workers were not 'fooled' by myrmecophilous lycaenid caterpillars which are known to suppress ant aggressiveness. All lycaenid larvae (3 taxa tested) were attacked and removed or killed
- *Cladomyrma* workers did not feed on the lepidopteran larvae they killed, instead, the dead larvae were thrown off the leaf
- cleaning behaviour was regularly displayed by *Cladomyrma* (tested in *maschwitzi* and *petalae*). Termite eggs placed onto young leaves were detected within the first hour and thrown off the leaf surface in 89% of all trials
- all *Cladomyrma* species tested (*dianeae*, *maschwitzi*, *petalae*, *yongi*) significantly reduced herbivore damage of young leaves
- as a rule, mature leaves of *Cladomyrma* host plants appeared to be less prone to herbivore attack but in one host plant (*Spatholobus bracteolatus*) they locally received conspicuous damage levels
- *Crematogaster* sp. 1, facultatively nesting in the tree *Saraca thaipingensis*, also reduced folivory on young leaves but significantly less effective than the obligate plant-ant *Cladomyrma petalae*

9.4. DISCUSSION

9.4.1. Protection against phytophagous insects

The results of my experiments clearly show that all *Cladomyrma* species tested (*andrei*, *dianeae*, *maschwitzi*, *petalae*, *yongi*) confer active anti-herbivore protection to young leaves of their host plants. Mean loss of leaf area was 2.6 (*Spatholobus*) to 7.9 (*Crypteronia*) times greater for experimental leaves (ants excluded) than for ant-patrolled leaves (controls). However, the controls showed that *Cladomyrma* ants cannot avoid at least low damage levels of immature leaves. In most controls, loss of leaf area is well below 10%, but rarely reaches 30% or more (maximum 77% in *Saraca*). The ant activity censuses (see chapter 8) revealed that the ants do not patrol leaves permanently, thus giving winged herbivores opportunities to feed on immature leaves for short periods.

Lepidopteran larvae were, in most cases, successfully removed from young leaves and field observations suggest that the presence of *Cladomyrma* workers may both discourage female lepidopterans from egg-laying and repel cicadas and leafhoppers that suck on young shoots (see p. 251). To my knowledge, protection against sucking insects has been demonstrated only once in an ant-plant mutualism (GAUME, MCKEY & ANSTETT 1997). Additionally, I never observed *Cladomyrma* workers tending membracids on the surface of their host. Host plant identity, hence indigestibility or toxicity of plant sap, cannot explain this observation since, in the absence of *Cladomyrma*, these membracids were often associated with various ant species on the same host plant species (e.g., *Crypteronia*, *Neonauclea*, *Saraca*).

Strikingly, *Cladomyrma* ants also never tended myrmecophilous lycaenid caterpillars which are known to suppress ant aggressiveness by appeasement substances (FIEDLER & MASCHWITZ 1988b, PIERCE et al. 2002). All lycaenid immatures encountered by *Cladomyrma* on young leaves were attacked and killed or removed from the leaf surface, thus providing an intriguing example for the limits of appeasement. This is in concordance with results obtained by SEUFERT & FIEDLER (1996) who examined the impact of *Cladomyrma petalae* on several myrmecophilous lycaenid species feeding on *Saraca thaipingensis*. While trees without *C. petalae* ants frequently serve as host plants for at least ten lycaenid species in Peninsular Malaysia (FIEDLER, HÖLLDOBLER & SEUFERT 1996), colonised trees are usually free of lycaenid immatures and, without exception, the ants attacked and killed all lycaenid larvae experimentally placed on leaf flushes of *S. thaipingensis*. Only one lycaenid immature is currently known to break the protective barrier imposed by *Cladomyrma petalae* living on *Saraca thaipingensis*. The flower-feeding specialist *Jamides caeruleus*

escapes predation by *Cladomyrma* ants through 'concealed feeding', even though the ant workers readily killed all *J. caeruleus* larvae offered during experiments (SEUFERT & FIEDLER 1996). The authors assume that *Cladomyrma*'s specific adaptations to myrmecophytism have led these ants away from the basic communication pathways which usually underlie trophobiotic symbioses between ants and lycaenids. In this respect, *Cladomyrma* ants are more effective against herbivores than the *Crematogaster* ant partners associated with certain myrmecophytic *Macaranga* plants where specialised lycaenid butterflies of the genus *Arhopala* are able to integrate into the ant-plant mutualism (MASCHWITZ et al. 1984, FIEDLER 1999).

The protection of young leaves varied considerably among host plants and associated *Cladomyrma* species. For example, the average rate of folivory in *Crypteronia griffithii*, inhabited by *Cladomyrma maschwitzi*, was 1.5% but reached nearly 9% in *Saraca thaipingensis* colonised by *C. petalae*. However, young leaves of ant-free *Saraca* twigs suffered distinctly greater mean herbivore damage (34.1%) than those of *Crypteronia* (11.9%), indicating that herbivore pressure differed between host plant species during the study period and/or that hosts differ in their direct chemical or mechanical defence.

I assume that *Saraca thaipingensis* is generally exposed to a rather high herbivore pressure. *Saraca* is a protein-rich plant as are most members of the plant order Fabaceae. Thus, such plants are especially attractive for herbivorous insects. In the absence of *Cladomyrma*, nearly all young leaves and shoots were infested with phytophagous insects. On young *Saraca* leaves I observed a large variety of chewing and sap-sucking insects, e.g., brenthid, curculionid, scarabeid, and chrysomelid beetles as well as cicadas and leafhoppers (Cercopidae, Cicadellidae, Flatidae, Membracidae, Nogodinidae, Ricaniidae, Tettigometridae, and Tomaspididae; MOOG 1991).

Lycaenid larvae also show a high tendency to prefer such protein-rich plants (PIERCE 1985). In Peninsular Malaysia at least 10 lycaenid species use *Saraca thaipingensis* as a food plant (FIEDLER, HÖLLDOBLER & SEUFERT 1996). One lycaenid, the obligate myrmecophilous *Anthene emolus*, stands out among lycaenid species in terms of herbivore damage inflicted on young *Saraca* leaves. When a *Saraca* tree is occupied by the weaver ant *Oecophylla smaragdina*, females of *Anthene emolus* use the presence of the symbiotic weaver ant as an oviposition cue (FIEDLER & MASCHWITZ 1989a). The authors reported that on a single *Saraca* bush (a cut stump with recently regenerated sucker shoots) nearly 4000 eggs were deposited in a period of 4 weeks. After adoption of the *A. emolus* larvae the weaver ants actively colonised every young

leaf of the *Saraca* bush with the larvae, so that all leaf flushes were severely damaged and sometimes completely destroyed (see also Fig. 9-5A).

Such potentially dramatic herbivore damage, caused by the interaction of *Oecophylla* with a specialist lycaenid, is not covered by my ant-exclusion experiments since I selected *Cladomyrma* occupied trees and excluded ants from patrolling young leaves by coating the twigs with a sticky resin. Thus, the impact of young-leaf protection of *Saraca* by *Cladomyrma* is probably underestimated. Does the presence of a *Cladomyrma petalae* colony on *Saraca thaipingensis* prevent the establishment of *Oecophylla smaragdina* on the plant? This question has not been tested but I observed a few encounters between *Cladomyrma* and *Oecophylla* under natural conditions. In all cases (n=4) the ants' behaviour was strongly antagonistic: (i) an *Oecophylla* worker captured a colony-founding female of *C. petalae* and killed it; (ii) three *Cladomyrma* workers attacked a single foraging *Oecophylla* worker and the fighting workers fell down to the ground; (iii + iv) on each of two host plants *Oe. smaragdina* had built two and three 'barrack nests' despite the hosts being inhabited by *Cladomyrma*. In both cases the *Cladomyrma* workers hid inside the hollow stem chambers and did not patrol the young leaves. *Cladomyrma* colony size was estimated to be about 1,000 and 3,500 workers, respectively; such a colony size is usually associated with intense patrolling activity. Even though I tried to release alarm recruitment in the two *Cladomyrma* colonies by shaking the branches the workers remained inside their nest. I attribute this highly unusual timidity to the presence of *Oecophylla*.

These observations suggest that a mature *Oecophylla* colony is competitively superior to a mature *Cladomyrma* colony but that a *Cladomyrma* colony may be able to fight off a single or a few foraging *Oecophylla* workers. Also, it appears plausible that colony-founding females of *Oecophylla* (which found their colony on the surface of a leaf) will hardly be able to establish a colony in the presence of a *Cladomyrma* colony. Thus, *Cladomyrma* likely reduces establishment of *Oecophylla* on *Saraca*. At present, however, the magnitude of young-leaf protection against the devastating impact of the *Oecophylla*/*Anthene* association cannot be assessed.

9.4.2. Cleaning behaviour

Cleaning behaviour of *Cladomyrma* workers may also contribute to the protection of the host plant. The termite-eggs experiments with two *Cladomyrma* species, *maschwitzi* and *petalae*, demonstrated that workers remove potentially harmful insect eggs. In addition, debris on the surface was dragged away until it could be dropped off the plant. Workers of all *Cladomyrma* species display a characteristic and stereotyped

behaviour while patrolling young leaves. The workers move slowly over the entire leaf surface and appear to survey the surface thoroughly (see p. 229). The significance of this behaviour is unknown. It may be interpreted in the context of 'cleaning' or 'resource-collecting' (for a detailed discussion of the latter see 8.4.6., p. 236). Some arboreal ants are known to search leaf laminae for epiphyllae, fungal hyphae and spores, or pollen (*Camponotus*, *Cephalotes*, *Echinopla*, *Polyrhachis*, and pseudomyrmecines; BARONI-URBANI & ANDRADE 1997, DAVIDSON 1997, DAVIDSON et al. 2003). If *Cladomyrma* ants clean the young leaves of their host from plant pathogens and epiphyllae, benefits may accrue to the host plant through an increase in photosynthetic rate, leaf longevity, or survival (FONSECA 1994, SANTOS 2000).

Cleaning behaviour is a common trait in many plant-ants (e.g., *Camponotus*: FEDERLE, MASCHWITZ & FIALA 1998b; *Crematogaster*: FIALA & MASCHWITZ 1990; *Pheidole*: LETOURNEAU 1983; *Pseudomyrmex*: JANZEN 1967, FONSECA 1994; *Tetraponera*: JANZEN 1972). LETOURNEAU (1983) first coined the term 'passive aggression' for regularly performed cleaning behaviour. She emphasised that removal of insect eggs alone, with only weakly pronounced aggression against herbivorous insects, can result in considerable protection of the host-plant. Later, LETOURNEAU (1998) showed for the *Pheidole–Piper* system that folivory, the classical parameter measured in ant-plant studies, is not necessarily the sole or main benefit conferred by ants to their host plant. Instead, pathogenic fungi (besides shoot borers) can have strong detrimental effects on ant-free myrmecophytic *Piper* plants. Correspondingly, HEIL et al. (1999, 2001a) reported that *Macaranga* ant-plants experimentally deprived of their symbiotic *Crematogaster* ants suffered heavily from shoot borers and pathogenic fungi.

The predominant mechanism of fungal establishment on leaves is wounding, such as that caused by herbivory, and fungal infection through direct contact is relatively rare (GARCIA-GUZMAN & DIRZO 2001, and references therein). Thus, two plant-ant traits, cleaning behaviour and anti-herbivore defence, can both be expected to reduce the incidence of infection by pathogens. However, it remains to be tested if *Cladomyrma* workers remove pathogen propagules as they patrol the surface of young leaves.

9.4.3. Does *Cladomyrma* provide protection against folivorous mammals?

There is no evidence that any *Cladomyrma* species is very effective in deterring herbivorous mammals. Although bites of *Cladomyrma* workers are irritating to humans, hundreds of bites can be tolerated if there is a compelling reason to invade the host plant. Records of mammals feeding on the foliage of *Cladomyrma* host plants are scarce. Several species of leaf monkeys (*Presbytis*) are known to feed on the fruits, seeds and leaves of species of the genera *Drypetes*, *Ryparosa*, *Saraca* and *Spatholobus* (DAVIES, BENNETT & WATERMAN 1988, WATERMAN et al. 1988). Larger herbivorous mammals, which potentially utilise host plants of *Cladomyrma*, may include e.g., gibbons and, in Borneo, orang-utans and elephants. [Native wild pigs are also known to negatively influence growth and survivorship of understorey saplings in Malaysia, however, these effects are not caused by herbivory but are due to stem-snapping (for nest building) and soil rooting (ICKES, DEWALT & APPANAH 2001).]

An example of the effectiveness of plant-ants defending their host tree against herbivorous mammals was reported by MCKEY (1974b) from Cameroon. A *Colobus satanas* monkey feeding on the foliage of unoccupied *Barteria* trees strictly avoided trees occupied by stinging *Tetraponera* ants, although *Barteria* leaves seemed to be a favourite food for this monkey. Even more intriguing is the note of KOHL (1909, p. 106) that it was customary in some parts of the country to punish unfaithful wives by tying them to *Barteria fistulosa* plants inhabited by 'Sima' (= *Tetraponera*) ants: "Mein schwarzer Diener erzählte mir eines Tages, daß man in seiner Heimat die Gewohnheit habe, die untreuen Frauen lebend an Sima-beherbergende Pflanzen anzubinden."

JANZEN (1972) suggested that several traits indicate the importance of large browsing mammals in the evolution of an ant-plant mutualism: (i) the workers accurately locate and approach large objects close or under the host tree, either by falling from the host plant or walking up from the ground; (ii) the workers do not immediately bite and sting, but rather walk about until a patch of bare skin is found and then attack; (iii) once the workers have found bare skin and grabbed on to bite or sting, they are very difficult to remove; (iv) the pain from a sting is heavy and long-lasting so that it produces memory (and avoidance) in the mammal; (v) the investment of ant colony biomass into workers is biased towards relatively few but large workers; and (vi) workers may release a strong odour when disturbed that does not produce alarm recruitment by the colony, but presumably serves as a warning sign to mammals.

In most parts these traits do not hold true for *Cladomyrma* ants. The rather small, formicine *Cladomyrma* species possess no sting – a defence which is usually more effective against mammals than bites. Only few, big-sized ant species are able to cut

deeply into human skin (such as certain *Camponotus* spp.). The pain caused by *Cladomyrma* bites is easily bearable and ephemeral; it certainly does not produce a long-lasting memory and avoidance behaviour in a persistent researcher. However, molested *Cladomyrma* workers, especially those of the larger species, are also surprisingly persistent. Some workers bite and spray formic acid many times and, after finding soft bare skin, do not release their hold. They can only be removed by firmly brushing the hands. The release of formic acid (or other additional chemicals) causes a strong alarm response in mature *Cladomyrma* colonies and several dozens of nestmates join in the attack. Major workers wandering over my clothes may finally reach the neck or umbilicus and surprise me, even after two hours, with a tiny sharp bite. These behavioural traits suggest that the small, non-stinging *Cladomyrma* ants have a certain degree of effectiveness against at least some folivorous mammals.

Support for this assumption comes from studies of MADDEN & YOUNG (1992) and STAPLEY (1998) who provided evidence that small, biting *Crematogaster* ants, inhabiting the swollen-thorn acacia *Acacia drepanolobium*, are able to slow down the rate of feeding in adult giraffes and effectively deter giraffe calves and goats. The latter showed a conspicuous response to the defending *Crematogaster* ants (STAPLEY 1998, p.404): "The animal shook its head and sneezed violently, using its hooves to remove ants that were biting its face." This observation points to an important difference in the susceptibility of mammals to attacks by small, biting ants. Browsing mammals such as goats or deer will be attacked on mouth and eyes without being able to brush off the ants easily. In contrast, monkeys (or humans) appear to be less susceptible to small biting ants because attacks will not strike the vulnerable face first, instead, the ants can be removed from the limps with the help of the hands.

To summarise, *Cladomyrma* ants are most effective against soft-bodied herbivorous insects such as caterpillars but, to a much lesser degree, they may also provide protection against some kinds of mammals. In mature colonies, alarm recruitment is strong and dozens of persistent *Cladomyrma* workers biting the face of a mammalian folivore certainly become a nuisance. This, in turn, presumably reduces feeding time.

9.4.4. Underestimation of the protective effect

This study probably underestimates the protective effects of *Cladomyrma* on their hosts. First, the tanglefoot insect glue applied to experimental twigs (to prevent access of *Cladomyrma* workers to young leaves) may also have excluded non-flying herbivores. Second, damage inflicted by sucking insects was not measured. GAUME, MCKEY & ANSTETT (1997) reported that 'homopterans' feeding on young expanding leaves may significantly affect photosynthetic surface by reducing leaf size at maturity. Third, workers of *Cladomyrma* appear to clean the leaf surface (see above), thus they potentially reduce infection by pathogenic fungi or colonisation by epiphyllae. Fourth, the presence of *Cladomyrma* ants may discourage female butterflies from egg-laying. For example, *Cladomyrma petalae*, inhabiting *Saraca thaipingensis*, appears to preclude oviposition by female lycaenids (SEUFERT & FIEDLER 1996; and own obs.). Since the experimental design excluded ants from only one twig of each individual host tree the presence of ants at neighbouring twigs and leaves may still deter female butterflies from egg-laying. The fact that ant presence per se can be enough to produce an avoidance response by ovipositing female butterflies has been demonstrated by FREITAS & OLIVEIRA (1996).

Last, and most importantly, short-term studies usually underestimate the herbivores' effects on plant fitness. Although short-term experiments are suitable to provide a rough estimate of the ants' ability to reduce leaf area loss, they cannot demonstrate the 'real' leaf damage over the entire lifetime of the leaf (LOWMAN 1992, FILIP et al. 1995) or the long-term effects of ant defence (LETOURNEAU 1998, ALVAREZ et al. 2001, HEIL et al. 2001a). In the latter study, ant-exclusion in *Macaranga bancana* (as '*M. triloba*') over a 40-d period amounted to a missing leaf area of only 2.6% versus 1.2% in controls. In the long-term study, however, conducted over the time span of one year, ant-free *M. bancana* trees lost, on average, about 80% of their total leaf area, while total leaf area of inhabited trees increased by about 40% within the same time span. Moreover, the long-term experiments in the *Pheidole–Piper* mutualism showed that initially similar levels of folivory between control (ants maintained) and ant-excluded plants diverged only after 2-3 months (LETOURNEAU 1998), thus indicating the need for long-termed experiments. It has also been demonstrated that, besides folivores, insects feeding on shoot tissue can be an important source of plant damage in *Endospermum* and *Macaranga* ant-plants (LETOURNEAU & BARBOSA 1999, HEIL et al. 2001a). In the latter, detrimental effects of shoot borers became fully obvious only after a time span covering at least half a year. Although one cannot conclude from short-term experiments on folivory that plants depend vitally on the ants' protective function, anti-herbivore defence by obligate plant-ants is usually visible within a time

span of several weeks (e.g., VASCONCELOS 1991, FIALA et al. 1994a, GAUME, MCKEY & ANSTETT 1997, FEDERLE, MASCHWITZ & FIALA 1998b).

This is in accordance with the results of my ant-exclusion experiments on protection against folivory by *Cladomyrma* ants. Within only three to six weeks, leaf-area loss in plants deprived of their ants had significantly increased compared to that of control plants. This indicates that longer study periods would likely result in much more severe levels of herbivory in ant-excluded plants. However, data from long-term experiments on *Cladomyrma* host plants are lacking, except for *Crypteronia griffithii*. Non-quantitative observations over a period of two years on saplings planted at the Ulu Gombak field station (West Malaysia) demonstrated that damage in ant-free saplings (n=5) was much more pronounced, leading in three cases to the death of the plant. In one of the dead plants the causal factor was infestation by shoot borers. [Note that these observations on *Crypteronia* are not simply transferable to all *Cladomyrma* host plants. In Ulu Gombak (West Malaysia), some unoccupied seedlings (30–50 cm in height) of *Saraca thaipingensis*, growing in unsuitable habitats, were observed to survive in a suppressed stage for at least two years without any visible above-ground damage. These seedlings had not produced any young leaves during this period.]

9.4.5. Protection by a facultative ant, *Crematogaster* sp. 1

In general, plants associated with obligate plant-ants (such as *Cladomyrma*) are known or presumed to be better protected by their ant partners than plants visited or colonised by facultative ant species that utilise plant rewards (nesting space or extrafloral nectaries) in an opportunistic manner (DAVIDSON & MCKEY 1993a, FIALA et al. 1994a, VASCONCELOS & DAVIDSON 2000, HEIL et al. 2001a, LINSENMAIR et al. 2001). Although several studies reported a significant protection against folivores by facultative ants (e.g., O'DOWD 1979, STEPHENSON 1982, FIALA et al. 1994a, DEL-CLARO, BERTO & REU 1996, KOPTUR, RICO-GRAY & PALACIOS-RIOS 1998, FUENTE & MARQUIS 1999, OLIVEIRA et al. 1999, DEJEAN et al. 2000a), few studies directly compared the anti-herbivore protection of facultative with obligate ants.

In West Malaysia, the population of the tree *Saraca thaipingensis*, regularly inhabited by *Cladomyrma petalae*, is occupied in part by several opportunistic *Crematogaster* ant species. One of these species, *Crematogaster* sp. 1, occurs sympatrically with *Cladomyrma* and is a common coloniser of *Saraca* in the Ulu Gombak valley along the river Gombak. This allowed the comparison of the relative protective efficacy of a mutualistic plant-ant (*Cladomyrma petalae*) and a facultative ant (*Crematogaster* sp. 1).

Of the 280 *Saraca* trees located in the studied area (about 2000 m^2), 53% were occupied by *Cladomyrma*, while 37.5% harboured *Crematogaster* ants (the remaining 9.5% were uninhabited trees). The colonisation pattern was not homogeneous among sites (see chapter 4, p. 52). *Saraca* trees inhabited by *Crematogaster* were predominantly found at the river bank in a small strip of ca. 5 m width on both sides along the river, and colonisation rate reached 70% in the river bank strip. In contrast, trees inhabited by *Cladomyrma* were mostly found away from the river bank deeper in the forest, and there colonisation rate was 86%. This difference in occupation pattern between the two ant species corresponded to differences in the height of occupied trees. Overall, *Crematogaster* sp. 1 was found in a significantly larger proportion of taller trees. For the experiments on protection against folivory, however, I selected *Crematogaster*-inhabited trees similar in height to those occupied by *Cladomyrma* ($median_{Clado}$: 4.25 m, $median_{Crem}$: 4.8 m; U-test, P = 0.4115).

Species of ant significantly affected the degree of herbivory. As expected, *Crematogaster* sp. 1 nesting facultatively in the tree *Saraca thaipingensis* had a less pronounced protective effect against young-leaf herbivory than the obligate plant-ant *Cladomyrma*, however, the difference to the controls was still significant (P = 0.0297, Mann-Whitney; Tab. 9-4). Comparison of folivory between *Crematogaster*- and *Cladomyrma*-inhabited *Saraca* trees was highly significant (P = 0.0003, Mann-Whitney). The paired design experiment on folivory revealed that young developing leaves on twigs free of nesting ants but with free access to extrafloral nectaries (EFN) suffered a significantly greater loss of leaf area than those which harboured *Crematogaster* ants ($mean_{EFN}$ 31.8%, $median_{EFN}$ 18.0% versus $mean_{Crem}$ 14.8%, $median_{Crem}$ 11.8%; P = 0.00227, Wilcoxon). Note that in this pairwise test, leaves of uninhabited twigs were open to opportunistic 'tourist' ants visiting the EFN as well as to *Crematogaster* sp. 1 ants nesting in neighbouring twigs on the same tree.

These results support the two hypotheses (i) that plants occupied by specific plant-ants are better protected by their ant partners than plants visited or colonised by facultative ant species, and (ii) that proximity of nest sites to young leaves positively influences the outcome of ant presence on herbivory levels.

Observations of worker activity and behaviour may help explain the difference between the effects of the two ant species. Both species attack and deter or kill insect herbivores encountered on leaves, but the activity of *Cladomyrma* workers on young developing leaves is higher than that of *Crematogaster* sp. 1 during a 24-h cycle. Even at night, *Cladomyrma petalae* usually maintains a 'night watch' on *Saraca* leaf flushes (see chapter 8). Although *Crematogaster* sp. 1 similarly has a higher worker activity on

young developing leaves than on mature leaves, the number of ants on developing leaves usually falls down to zero during the night (pers. obs.). Apparently, the number of *Crematogaster* ants on leaf flushes of *Saraca* is synchronised with the timing of increased extrafloral nectar supply which peaks at mid-day. In contrast, *Cladomyrma* ants display a striking preference for young plant tissue in their patrolling activity independent of the extrafloral nectar. Exploitation of EFN by *Cladomyrma* does not occur under natural conditions; it could only be released in colonies under experimentally induced starvation (see p. 219). This preference for developing plant tissue appears to be of fundamental importance for the potential benefit *Cladomyrma* ants provide for their host, and I propose to term it 'neophily' (see 8.4.3., p. 232). Since insect herbivores active at night are a common threat to young *Saraca* leaves, the temporally more restricted worker activity of *Crematogaster* compared to *Cladomyrma* is probably one factor accounting for the lower efficacy in antiherbivore protection.

Moreover, pattern of visitation of young leaves differ between the two, similar-sized, ant species. Whereas *Cladomyrma* workers patrol the entire leaf lamina and seem to 'clean' the surface, *Crematogaster* ants mostly move along the leaf margin to check the EFN for nectar droplets. Other differences between the two species of ants include, e.g., colony-founding behaviour, host specificity, host fidelity, foraging activity, pruning behaviour, nest structure, and proportion of twigs inhabited on a tree (see chapter 4, p. 53).

The latter trait may constitute another important factor affecting protection against folivores. Mature *Crematogaster* sp. 1 colonies are polydomous and they usually do not occupy entire trees. Rather, they maintain separate nest chambers in a single or a few branches in each of several neighbouring plants, and use vines or climbers as bridges between nest parts. As a result, EFNs active on developing leaves are not necessarily in close proximity to their nest chambers, hence ant presence at EFNs is probably subject to a considerable degree of variation. Thus, the hypothesis that the outcome of biotic defence of plants will likely be diffuse or unpredictable if ant visitors to EFNs vary in space and time (see BARTON 1986, BRONSTEIN 1994, ALONSO 1998, RICO-GRAY et al. 1998, DI GIUSTO et al. 2001, HOSSAERT-MCKEY et al. 2001, MOOG, FELDHAAR & MASCHWITZ 2002) is supported by this study.

9.4.6. Is degree of folivory a good precursor of plant fitness?

Response to herbivory varies greatly in plants. Differences in intensity or frequency of defoliation between species do not necessarily translate into differences in survival or growth. Several species appear to be very successful in overcoming a high defoliation pressure because of their regrowth capacity (MEIJDEN, WIJN & VERKAAR 1988, TIFFIN

2000). Although a growing body of evidence indicates that tissue removal by herbivores, in general, is detrimental to plant fitness (see reviews by MARQUIS & BRAKER 1994 and BIGGER & MARVIER 1998), herbivore damage does not necessarily affect seed production and mortality (e.g., BECKER 1983, LETOURNEAU 1993, RUHREN 2003). However, even when plants appear to fully compensate for herbivory in the short term, past herbivore pressure can be negatively associated with net growth (GADD, YOUNG & PALMER 2001, OSIER & LINDROTH 2004). Thus, an effect of herbivory on fitness may become apparent only in long-term studies.

Studies on whether mutualistic plant-ants enhance the sexual reproduction of their host plants are extremely rare, presumably due to both the often late onset of reproduction in the ontogeny of host plants and logistical problems and/or restricted financial provisions concerning long-term studies in the tropics. For obligate ant-plant interactions, positive effects of ant tenancy on seed set have been demonstrated for *Acacia*, *Piper* and *Macaranga* ant-plants (WILLMER & STONE 1997, LETOURNEAU 1998, MOOG 2002). For facultative ant-plant interactions, mediated by extrafloral nectaries (EFN) on leaves, beneficial effects on plant reproduction by EFN-visiting ants are less scarcely reported (HORVITZ & SCHEMSKE 1984, DEL-CLARO, BERTO & REU 1996, SOBRINHO et al. 2002, and VESPRINI, GALETTO & BERNARDELLO 2003; but see RUHREN 2003).

Another level of complexity in the interplay of plant-ants and ant-plants occurs in systems where the associated ants provide protection against herbivory but nevertheless destroy the flowers of their hosts under certain circumstances (YOUNG, STUBBLEFIELD & ISBELL 1997, YU & PIERCE 1998, STANTON et al. 1999, MERBACH et al. 2001a, GAUME, ZACHARIAS & BORGES 2005, IZZO & VASCONCELOS 2002, MOOG 2002). The hypotheses given to explain this 'parasitic' behaviour in otherwise mutualistic ant partners are heterogeneous and will not be treated here (see chapter 10, p. 283, for a more detailed discussion).

The often strong positive effects on plant growth and survival provided by the activities of associated plant-ants are partly due to the importance of ant defence against shoot borers and pathogenic fungi (LETOURNEAU 1998, LETOURNEAU & BARBOSA 1999, HEIL et al. 2001a, PALMER et al. 2008). This illustrates that the ants' protective function against folivores may be of lesser importance than their defence against shoot borers or pathogens. However, I wish to point out that even low levels of folivory can negatively affect plant growth and reproduction, e.g., in a tropical understorey pepper plant *Piper arieianum* (MARQUIS 1984), and that plant wounds caused by herbivores provide opportunities for infection by fungi and other plant diseases.

In addition, herbivory on young developing leaves can greatly increase abscission rate as demonstrated for the dipterocarp tree *Shorea hopeifolia* (BLUNDELL & PEART 2000). If an increased abscission rate is a common response to young-leaf herbivory in plant species, it may contribute substantially to the cumulative impact of herbivory on growth and survival of whole plants. Therefore, I think that short-term experiments on folivory alone in an ant-plant association are a justifiable method in making a first estimate of the potential protection an ant confers to its host. Nevertheless, more studies are required to assess the relative importance of *Cladomyrma*'s impact on herbivores other than chewing insects, e.g., leaf miners, sap suckers, shoot borers, and pathogens.

Another, mostly neglected benefit of protective plant-ants to their hosts may lie in their capacity to keep juvenile understorey plants in 'good health' during periods of suppressed growth, thus increasing the ability for regrowth (rather than directly increasing plant reproduction). Juvenile plants may get through long periods without substantial growth (DELISSIO et al. 2002). Colonised saplings of *Crypteronia griffithii* growing under unfavourable low light showed very little growth during a two-year period (unpubl. results), suggesting that the mutualism with ants may help increase their ability to react to altered light conditions. An ant-inhabited juvenile plant with more and (nearly) undamaged leaves should better respond to improved growth conditions. CLARK (1994) recorded that juvenile performance of non-pioneer trees (in Costa Rican tropical rainforest) showed (i) growth responses to small increases in light, (ii) the capacity for substantial growth in high light, and (iii) the ability to survive years without growth. This gains importance by the fact that in most cases the juveniles of shade-tolerant tree species in tropical rainforests, rather than germinating dormant seeds, replace canopy adults (UHL et al. 1988, SCHUPP et al. 1989).

9.4.7. Plant defence hypotheses

Plants are known to benefit from anti-herbivore defences provided by other organisms, mainly arthropods (DE MORAES et al. 1998, AGRAWAL & COLFER 2000, CORTESERO, STAPEL & LEWIS 2000). Protection from herbivores by entomophagous arthropods, such as parasitoids and predators that use herbivores as hosts or prey, can be so striking that they are sometimes referred to as 'plant bodyguards' (DICKE & SABELIS 1988). In this type of defence system, which is called **biotic defence**, plants attract or nourish other organisms so that they will protect them from herbivore attacks. In the tropics, numerous plant species use ants for anti-herbivore defence, either by attracting 'tourist' ants to food rewards on their surface or by providing food and housing for specialised ants (SCHUPP & FEENER 1991, DAVIDSON & MCKEY 1993a, FIALA & SAW 2003, MOOG et al. 2003).

In addition to biotic defence, plants usually protect themselves against herbivores (and pathogens) by producing (i) chemical defences such as toxins, repellents and digestibility reducers, and (ii) physical defences such as spines, trichomes, waxes, thick cell walls and fibres. Phenological mechanisms such as the unpredictable or pulsed production of young leaves may also contribute to plant defence by escaping from, or satiating young-leaf herbivores. These types of defence mechanisms may be called direct defence mechanisms, as opposed to indirect biotic defences. For both biotic and chemical/physical defences plants have to allocate photosynthetic products and nutrients to processes other than growth and reproduction (SIMMS & RAUSHER 1987). Hence, these types of defence mechanisms impose costs on the plants.

Before discussing biotic defence in *Cladomyrma* host plants, I would like to recapitulate briefly some established hypotheses about the relative investment in defence in order to set biotic defence in its functional context. In plant defence hypotheses, the emphasis is on vulnerability and fitness value (MCKEY 1974a, 1979), apparency (FEENY 1976), productivity (COLEY, BRYANT & CHAPIN 1985), the degree of neutral resistance (EDWARDS 1989), or scarcity and accessibility (GRUBB 1992).

The '**optimal defence hypothesis**' (MCKEY 1974a, 1979; RHOADES 1979) states that secondary compounds are costly to the plant and, consequently, their location and concentration in plants is governed principally by two factors – a tissue's vulnerability and its fitness value to the plant. The value of a plant tissue is determined by the reduction in fitness of the plant that results from the loss of that tissue. Such costs are not fixed; if resources are in short supply, the ability of a plant to replace lost tissue will be diminished. Stated in its simplest form, the hypothesis predicts that selection will favour defence when the benefit of that defence exceeds its costs. Although these ideas have been expanded since their publication, the basic premise remains intact.

The '**apparency hypothesis**' focuses on conspicuousness. FEENY (1976) argues that plants or plant parts (e.g., young leaves) less easily detected by a herbivore are less likely to suffer damage, and hence are less likely to possess defences. These less 'apparent' plants or plant parts are expected to have 'qualitative' defences (such as alkaloids) which are toxic or deterrent to generalist herbivores. In contrast, highly 'apparent' plants or plant parts in terms of space (covering a large part of the landscape) or time (long-living) are "bound to be found" by their specific herbivores and thus require strong 'quantitative' chemical defences (notably tannins) which effectively reduce nutritive value.

The '**resource availability hypothesis**' (COLEY, BRYANT & CHAPIN 1985) maintains that fast-growing plants have less need to defend themselves than resource-limited plants. Plants which grow at resource-poor sites and are less able to recover after partial defoliation are expected to invest more heavily in defence, particularly in 'immobile' defences such as thick cell walls and tannins, which have low maintenance costs and are not withdrawn from senescent parts. Plants which grow under resource-rich conditions can more easily replace tissue lost to herbivores and are thus expected to invest less in defence. These plants are expected to have 'mobile' defences such as alkaloids and terpenoids which are believed to have high maintenance costs (must be constantly synthesised) but are capable of withdrawal at senescence.

The '**neutral resistance hypothesis**' (EDWARDS 1989) treats important features regarded by other authors as 'defences' as parts of the neutral resistance of a plant. EDWARDS (l.c.) drew a distinction between plant traits which convey 'neutral resistance' and those which convey specific 'defence' against animals. Plant traits conveying 'neutral resistance', such as thick cell walls or bands of fibres in the leaf, may be of value to the plant in respect of many different physical hazards and in reducing penetration by pathogenic micro-organisms as well as deterring herbivores. Tannins are also as effective against fungi as against animals. The nearest to pure defences against herbivorous animals are chemical defences such as alkaloids, terpenoids or glucosinolates. This notion leads to the assumption that plants with greater neutral resistance are generally more primitive and slower-growing, whereas plants with less neutral resistance are more advanced; they need and have greater amounts of true chemical defences.

The '**scarcity-accessibility hypothesis**' (GRUBB 1992) states that previous hypotheses intended to explain the development of anti-herbivore defences are inadequate because they are concerned with just one axis of variation. Instead, several variables need to be considered: productivity, accessibility and proportion of the landscape covered, architecture, seasonal behaviour relative to neighbours, nutrient concentration relative to neighbours, and kinds of herbivore present. This hypothesis, tested through an examination of the distribution of spines in plants, claims to account for completely opposite kinds of plants being armed, for example, particularly slow-growing and particularly fast-growing plants, or the deciduous species in one system and the evergreen in another.

The reasoning for the productivity dimension, for example, is as follows: Where there is scarcity of accessible nutritious material at the landscape scale (e.g., in a dry-climate area) the chance of spines evolving will be high because edible material is

scarce throughout and accessible to ground-based vertebrate herbivores throughout the life-time of each plant. In a wet-climate evergreen forest, highly productive plants near the ground (accessible to ground-based herbivores) are confined to tree-fall gaps, forest edges and river banks and are therefore relatively scarce. Here, the desirable plant material is scarce not because the whole landscape is unproductive but because gaps occupy only 1-10% of the area (and edges even less).

GRUBB (1992) emphasises the importance of the 'plant architecture' dimension to explain the distribution of spines in plants. Many species within four groups of plants typical of the tropical rainforests (pandans, palms, tree-ferns and bromeliads) are spiny despite being able to grow in shade. According to GRUBB (l.c.) they are widespread in the forest rather than confined to relatively scarce tree-fall gaps or forest edges. A trait common to pandans, palms, tree-ferns, and bromeliads is the scarcity of apices. In most of these plants, damage to the single apical meristem means death for the plant. Thus the apices are in short supply and, without regard to growth rate or resource availability, it appears to be generally advantageous to such plants to have spines. It should be noted that rattans, spiny climbing palms in tropical forests of the Old World, often form associations with ants, and many of the morphological features that provide ant domatia are shared between the Asian and African taxa (SUNDERLAND 2002).

9.4.8. What is the role of biotic defences in relation to the plant's other defences?

Based on previous considerations of JANZEN (1966) and REHR, FEENY & JANZEN (1973), MCKEY (1988a) was the first to put biotic defence mediated by ants in the context of general hypotheses about plant anti-herbivore defence systems. He reasoned that leaves protected by defences such as tannins and lignin have very low maintenance costs. However, such defences cannot be reclaimed and are lost when leaves are shed. But since the benefit of this non-reclaimable investment increases with leaf life-span, non-reclaimable defences are best suited for plants with long-lived leaves. In contrast, reclaimable or mobile defences, usually small toxic molecules such as alkaloids and terpenoids, are metabolically active and impose high maintenance costs to the plant. This type of defence is more expensive for the protection of long-lived leaves, and thus it is restricted to plants with short-lived leaves or rapid leaf turnover.

According to MCKEY (1988a) biotic defence by ants functionally resembles mobile, reclaimable chemical defences and must be viewed in an overall functional context. Thus, biotic defence is encouraged when constraints on alternative defences open to the plant are stronger than those on biotic defence. It is predicted that myrmecophytes

occur either in fast-growing plants of second-growth with high leaf turnover (maintenance costs of ants are high but do not exceed those of mobile chemical defences) or in shade-tolerant plants with long-lived leaves. In the latter, biotic defence does not necessarily replace chemical/physical defence of mature leaves because maintenance of a worker force would be more expensive than a non-reclaimable investment in tannin and lignin. Instead, a small worker force exclusively protects the young, expanding leaves, which are difficult to defend chemically or mechanically (see below). In other words, a division of function between biotic defence and chemical/physical defence according to leaf age is expected.

The idea that biotic defence in ant-plants will exhibit patterns of distribution similar to those of mobile chemical defences has been extended and refined by AGRAWAL & DUBIN-THALER (1999), HEIL et al. (2001a), and LINSENMAIR et al. (2001), who proposed that plant-ants can be viewed as an inducible defence for their host plants because of their rapid and aggressive recruiting ability to those parts of the plant surface which actually require defence, their reclaimable and redeployable nature, and their protective effect against many types of insects, climbers, and pathogens. Thus, they fulfil several functions for which otherwise a variety of different chemical substances would be necessary.

9.4.9. Vulnerability of young plant tissue

"Herbivores do not eat latin binomials". JANZEN's (1979, p. 336) statement points to an important aspect of protection mutualisms in ant-plants. It means that herbivorous animals generally do not feed on *all* parts of a plant; they usually consume quite specific parts. Thus, the record of a herbivore feeding on a Latin binomial (e.g., *Saraca thaipingensis*) carries little information when it is remembered that plants as a whole do not possess chemical or physical defence, but rather plant parts do.

Young foliage, for instance, is difficult to defend, because (i) expanding young leaves cannot be lignified, (ii) storage space for potentially autotoxic allelochemicals is limited, and (iii) high nutrient content requires high concentrations of defence to discourage herbivores (MCKEY 1979, HAGERMAN & BUTLER 1991). Although young leaves sometimes contain higher concentrations of chemical defences than mature leaves (phenolics: COLEY 1983, alkaloids: VAN DAM et al. 1996), young leaves are usually more nutritious and less tough and fibrous (COLEY 1983, DAVIES, BENNETT & WATERMAN 1988, COLEY & BARONE 1996, BLÜTHGEN & METZNER 2007). This probably explains why, in general, the rate of herbivory on soft, expanding leaves is considerably higher than on mature, fully expanded ones (e.g., ORIANS & JANZEN 1974, COLEY 1983, WINT 1983, ERNEST 1989, NICHOLS-ORIANS & SCHULTZ 1989,

FONSECA 1994, BARONE 1996, BASSET 2001, CORNELISSEN & FERNANDES 2001a, MARQUIS, DINIZ & MORAIS 2001).

Another important aspect is that young shoots and leaves have a high potential value for the plant. The loss, for instance, of a certain amount of young-leaf area means an entirely different thing to the plant than the same loss of leaf area after the leaf has been amortised (JANZEN 1979, HARPER 1989). I thus hypothesise that the general vulnerability of young tissue (foliage and shoot tips) to herbivores is one of the main constraints leading to the evolutionary development of traits facilitating biotic defence by ants in tropical plants. For natural herbivory in tropical rainforests leaf toughness has been shown to be the most important correlate of damage levels (COLEY 1983, MARQUIS & BRAKER 1994). As discussed above, toughness of leaves is rather slow to develop and difficult to implement in young foliage, thus rapid onset of biotic defences during new leaf development is expected to strongly reduce herbivory on young leaves. This requires that plants direct 'bodyguards' to vulnerable plant structures.

9.4.10. The role of extrafloral nectaries

Ant-attracting extrafloral nectaries (EFN) are very widespread among terrestrial plants and occur in species from groups as divergent as ferns and legumes (e.g., ELIAS 1983, KEELER 1989, BALGOOY 1997). In subtropical Southeast Asia, species with EFN make up a remarkable 7.5% of the flora (PEMBERTON 1998). Even more striking are the results obtained from a primary lowland rainforest in Malaysia. In the 50 ha plot at Pasoh Forest Reserve, EFN were present in 12.3% of the 741 tree species surveyed and comprised 19.7% of all tree individuals (FIALA & LINSENMAIR 1995, FIALA & SAW 2003). Comparable levels of EFN-cover were reported from the Neotropics and African tropics (MORELLATO & OLIVEIRA 1991, MCKEY 1992). The highest figure reported to date for any flora was found on Barro Colorado Island in Panama. About one-third of the 243 plant species surveyed were EFN-bearing plants (SCHUPP & FEENER 1991).

In most cases, EFNs have a spatio-temporal relation to young-leaf production. First, extrafloral nectar is usually secreted in young developing leaves and its production ceases with maturation of the leaves. Second, the location of EFNs is usually restricted to the leaf lamina, leaf margin or petiole, that is, close to or directly at the vulnerable, developing plant tissue. These traits may indicate that plants evolved EFN to gain young-leaf protection by ant 'bodyguards'. Recently, however, the hypothesis that EFNs evolved (in part) to protect the plant against destructive ant-hemiptera associations (BECERRA & VENABLE 1989) has found renewed interest (DAVIDSON &

COOK 2003; but see opposing opinions by FIALA & MASCHWITZ 1991, N. BLÜTHGEN, pers. comm.).

In most obligate ant-plant mutualisms, the ants cultivate trophobionts and EFNs are absent, e.g., in *Cecropia*, *Macaranga* (in part), *Tachigali*, *Triplaris*; and exceptions are relatively rare, e.g., *Acacia* and *Leonardoxa*. For a few obligately myrmecophytes the presence of active nectaries on young leaves appears to be an ambiguous character. For example, all obligate *Macaranga* ant-plants possess EFN-like glands at the margin of young leaves but, according to FIALA & MASCHWITZ (1991), the sugar content of these glands is extremely low or absent. The authors suggest that these structures function as hydathodes. However, semi-quantitative quick tests with Dextrostix (Merck) sometimes yielded measurable sugar concentrations of the secreted liquid in very young developing leaves of myrmecophytic *Macaranga hullettii* (U. MOOG, pers. comm.). Presumably, secretion of nectar in marginal glands is restricted to the earliest phase of leaf development or is confined to *Macaranga* plants with waxy stems (W. FEDERLE, pers. comm.). Alternatively, EFN production may be responsive to varying levels of herbivory and represents an 'inducible defence'. Recent studies have demonstrated that some EFN-bearing plants can regulate both the amount and/or quality of the nectar secreted and even the number of visually conspicuous EFN (HEIL et al. 2001c, WÄCKERS et al. 2001, MONDOR & ADDICOTT 2003, NESS 2003).

Another ambiguous case concerning EFNs are the African myrmecophytes in the genus *Barteria*. JANZEN (1972) and YUMOTO & MARUHASHI (1999) report that in the obligate *Barteria fistulosa* – *Tetraponera aethiops* association the ant colony depends on scale insects and, presumably, fungus gardens for food. EFNs are not mentioned. This is in contrast to KOHL (1909, p. 106) who observed ants licking the EFN of *B. fistulosa*.

Indeed, all species of *Barteria* (including *B. fistulosa*) have extrafloral nectaries situated on the decurrent petiole margins (BRETELER 1999). Several factors may explain why some authors failed to observe either these glands or the attraction of ants to them. First, in *B. fistulosa* (and *B. dewevrei*) they are only found on the orthotropic (vertical) shoot. The plagiotropic shoots in which the domatia are located are free of EFN (BRETELER 1999). Second, nectar secretion may be restricted to a short period during leaf development. Third, sugar concentration may be so low that resident ants are not attracted to the EFNs when having 'normal', superior food supply (scale insects). And fourth, *Tetraponera aethiops* destroys foliar nectaries. Indeed, *T. aethiops* is known to prune shoot tips of its host (YUMOTO & MARUHASHI 1999) and another *Tetraponera* plant-ant, *T. penzigi*, has been observed to cut off virtually all

EFN of its *Acacia* hosts; a behaviour that is suggested to reduce the probability of aggressive takeover by competing ants attracted to EFN (PALMER, YOUNG & STANTON 2002). Notwithstanding these uncertainties, the general preference in ant activity for young plant tissue of *Barteria* is undisputed.

FIALA & MASCHWITZ (1991) proposed that lack or reduction of nectar production by EFNs in obligate ant-plants helps stabilise the maintenance of specific associations, because it prevents or reduces competition of resident plant-ants with opportunistic 'tourist' ants. The *Leonardoxa africana* subsp. *africana* case may support this hypothesis. Although this host plant, associated with the obligate plant-ant *Petalomyrmex phylax*, possesses EFN, the production of nectar (apparently an essential part of *Petalomyrmex*'s diet) is restricted to a very short period during mid-day (GAUME & MCKEY 1999). The short pulses of extrafloral nectar production in *Leonardoxa* likely reduce encounters of *Petalomyrmex* with alien ants. Similarly, the extrafloral nectaries of the New Guinean myrmecophyte *Endospermum medulosum* are inactive for most of the diel cycle but during a short period at night they produce large droplets of EFN, which resident nocturnal *Camponotus quadriceps* quickly deplete before competitors arrive (DAVIDSON & MCKEY 1993).

A special case is the mutualistic association between the carnivorous pitcher plant *Nepenthes bicalcarata* and the specific plant-ant *Camponotus schmitzi* which lives in the tendril domatia (SCHUITEMAKER & STÄRKE 1933). *Nepenthes bicalcarata* possesses a high number of EFNs distributed over the whole leaf lamina and the pitcher trap. However, the production of extrafloral nectar is neither shortly pulsed nor confined to a short phase during leaf ontogeny, thus the EFN secretions are constantly accessible for both the specific ant partner and opportunistic ant visitors (MERBACH et al. 2001b).

According to MERBACH et al. (2007) the EFNs in *N. bicalcarata* serve a double function, i.e., attraction of potential prey and, at the same time, nourishment of ant bodyguards. At first, this appears to be a contradiction because obligate ant partners are expected to hinder the access of potential prey. However, the specific ant partner *C. schmitzi* is surprisingly inaggressive against visiting ants and generally exhibits a low activity on the plant surface (MERBACH et al. 2001c). In addition, workers of *C. schmitzi* feed mainly on the slippery giant nectary thorns which are hardly accessible to other ants. These traits help reduce aggressive encounters with alien ants. Yet *C. schmitzi* is an effective biotic defence agent for *N. bicalcarata* because it significantly reduces herbivore damage by attacking a specific trap-destroying weevil (MERBACH et al. 2007). Whereas opportunistic 'tourist' ants visiting EFNs of *N. bicalcarata* may get trapped in the pitchers, *C. schmitzi* workers are able to walk on the slippery pitcher

walls and even retrieve prey items from the pitchers (CLARKE & KITCHING 1995). MERBACH et al. (2007) hypothesise that in *N. bicalcarata* prey catching and protection against herbivores represent a delicate equilibrium state.

Despite the lack of EFNs in many obligate ant-plant symbioses the associated ants usually exhibit a preference in their patrolling activity for young foliage. Here, the patrolling activity appears to be decoupled from the distribution of food sources (for a detailed discussion of this subject see chapter 8). It is emphasised here that even though the proximate factors of ant attraction to young plant tissue in obligate ant-plant mutualisms are largely unknown, the concentration of ant activity on young vulnerable plant parts is a common and striking pattern in both facultative and obligate ant-plant association. I hypothesise that this pattern generally reflects the vulnerability of young foliage and its fitness value to a plant.

9.4.11. Biotic defence by *Cladomyrma*

The strong preference of *Cladomyrma* for patrolling young plant tissue ('neophily') is linked to a significant protection of young leaves against herbivorous insects. Do these findings help verify certain hypotheses of plant defence against herbivore damage?

Protective ant-plant interactions are considered to present good models to test hypotheses of plant anti-herbivore defence (MCKEY 1988a, DAVIDSON & FISHER 1991, HEIL & MCKEY 2003). In contrast to direct chemical defences that pose high barriers to experimentation, ants as indirect, biotic anti-herbivore defence are "worn on the outside" of the plant, thus they can be experimentally removed from the plant to allow tests of their effectiveness. Above, I have focused on some of the currently established plant defence hypotheses, with emphasis on optimal defence, apparency, resource availability, neutral resistance, and scarcity-accessibility. Also, I highlighted the general vulnerability of young leaves to herbivore attack and suggested –by using EFN as an example– that it is likely one of the major constraints leading to the evolutionary development of traits facilitating biotic defence by ants in tropical plants. In the following I wish to show that the patterns observed in the *Cladomyrma*/plant associations are (i) most consistent with the 'optimal defence hypothesis' which states that defences should be concentrated in the most valuable and vulnerable parts of a plant (MCKEY 1974a, 1979), but (ii) that there are limits to apply these patterns to other plant defence hypotheses.

Mature leaves of most host plant taxa of *Cladomyrma* appear to experience relatively little herbivore damage compared to young ones, e.g., in *Crypteronia*, *Drypetes*, *Luvunga*, *Ryparosa*, and *Strychnos* (but see *Spatholobus bracteolatus*, p. 256). These

plant taxa grow, at least as saplings, in the understorey or in slightly disturbed habitats of intermediate light regime such as in small forest gaps and along logging roads or river banks. The most shade-tolerant host species are probably those of the genera *Ryparosa* and *Strychnos*, followed by *Luvunga*, *Drypetes*, *Saraca*, *Spatholobus* and *Callerya*. In contrast, myrmecophytic species of the genus *Neonauclea* are mostly conspicuous early successional or pioneer trees common in (highly) disturbed forests, on open slopes, forest edges, and along river banks and road sides. They appear to generally receive higher levels of adult-leaf herbivory than other *Cladomyrma* hosts. However, data on leaf area loss of mature leaves from all *Cladomyrma* host plants are needed to verify these non-quantitative observations. It is noteworthy that saplings of some myrmecophytic *Neonauclea* species can also grow at low light levels in the understorey.

Across all taxa, *Cladomyrma* host plants show considerable ecological amplitude ranging from lowland to hill mixed dipterocarp forests (up to ca. 1,300 m) and from limestone to swamped forests or riparian fringes. In addition, abundance of *Cladomyrma* host taxa is extremely variable; for example, *Luvunga* sp., *Ryparosa fasciculata*, *R. porcata*, *Drypetes longifolia*, *D. fusiformis* and *Crypteronia macrophylla* are (very) rare or uncommon plants, others have a scattered distribution (*C. griffithii*) or are locally common (e.g., *Saraca thaipingensis*, *Spatholobus oblongifolius*). Only few host species may be common (some *Neonauclea*) or even gregarious, occasionally forming monospecific stands (*N. gigantea*).

To sum up, *Cladomyrma* host plant taxa differ strongly with respect to light regime, forest types, soils, altitudinal range, growth form (tree or woody climber), abundance and distribution. This ecological heterogeneity may even be present among host plants of a single *Cladomyrma* species. *C. petalae* inhabits 6 host taxa from the genera *Drypetes*, *Luvunga*, *Ryparosa*, *Saraca*, *Spatholobus*, and *Strychnos*, which all differ strongly in ecological traits. This striking heterogeneity of *Cladomyrma* host plants, however, is not reflected in differing protective activities between *Cladomyrma* species. On the contrary, the ants' behaviour appears to be remarkedly uniform with respect to activity pattern, neophily, cleaning, pruning, and herbivore attack. According to present knowledge, *Cladomyrma* species all display the same set of behavioural traits linked to the protection of the host, and only gradual differences in the performance intensity of some traits among species are known (see *C. maschwitzi*, p. 293).

Although the host plants differ in many important factors –such as resource availability, apparency, scarcity-accessibility, etc.– which are hypothesised to

influence the type of defence and its spatial and temporal occurrence within the plant, *Cladomyrma* ants concentrate their protection activities to young plant tissue, thereby providing indirect biotic defence for plant parts – irrespective of host taxon or habitat – that are generally the most vulnerable and valuable parts of a plant. The biotic defence mechanism of *Cladomyrma* ants is thus consistent with the concept of 'optimal defence' which states that the location and concentration of plant defences is principally governed by a tissue's vulnerability and its fitness value for the plant. Recently, this concept has also been applied to the *Crematogaster/Macaranga* mutualisms (HEIL et al. 2004b).

Other plant defence hypotheses, however, such as the 'resource availability hypothesis' cannot be supported by the available evidence regarding *Cladomyrma*'s plant protection. This hypothesis states that fast-growing plants have less need to defend themselves than resource-limited plants (COLEY, BRYANT & CHAPIN 1985). Plants which grow under resource-rich conditions can more easily replace tissue lost to herbivores and are thus expected to have 'mobile' defences such as alkaloids or other small molecules which are believed to have a high turnover rate (maintenance costs are high) but can be reclaimed from leaves before they are shed. It is thus predicted that such defences occur mainly in short-lived leaves of fast-growing plants. Plant-ants resemble such 'mobile' defences; they can move easily over the plant surface and are not lost when leaves are shed. In contrast, plants which grow at resource-poor sites are expected to invest more heavily in 'immobile' defences such as thick cell walls and tannins, which have low maintenance costs but are not withdrawn from senescent leaves. These defences are predicted to be present in long-lived leaves of shade-tolerant plants. Biotic defence mediated by ants is thus not required for mature, older leaves, but it may still be beneficial for young, developing leaves which are difficult to defend chemically or mechanically (MCKEY 1988a).

Superficially, these considerations are consistent with the patterns observed in the biotic defence mechanism of *Cladomyrma*. Furthermore, 'mobile' ant defences are highly developed in pioneer trees of both the New and Old World, a fact that appears to correspond with the resource availability hypothesis which predicts 'mobile' defences in short-lived leaves of fast-growing plants. However, it does not explain why worldwide ant defences are almost exclusively concentrated on young leaves, irrespective whether the host plants are early successional or shade-tolerant.

To my knowledge, there have only been three reported exceptions ever to this general rule. In the *Maieta*/*Pheidole* association, ant patrolling of leaves was independent of leaf age, presumably because leaves of both ages are equally susceptible to

herbivore attack (VASCONCELOS 1991). Similarly, patrolling of *Tococa bullifera* by its two ant partners, *Azteca* sp. and *Crematogaster laevis*, was not significantly different between new and mature leaves, although there was a tendency for stronger patrolling of new leaves (BRUNA, LAPOLA & VASCONCELOS 2004). Leaves of both age classes experienced high rates of herbivory, however, mature leaves of *Tococa* were less well defended than new ones by both ant species. The special case of the *Nepenthes/Camponotus* mutualism has already been discussed above (MERBACH et al. 2001b; see page 277). Another problem in applying this model occurs due to the rather rigid subdivision of plants into 'pioneers' and 'shade-tolerants' which does not reflect the variability seen among and/or within plant taxa ('optimal' light levels change during ontogeny).

Has the importance of 'animal-specific' traits in indirect plant defences been generally underestimated? *Cladomyrma* may provide an example for this assumption. First, if 'neophily' is an ancestral trait in *Cladomyrma* (as suggested by its occurrence in all members of the genus) and provides a potential benefit to the plant, it could be passed on to, and retained in, newly acquired hosts. The fact that host shifts or host additions must have occurred several times in the evolutionary history of *Cladomyrma* is indicated by the extremely broad host range of the genus. If, secondly, a potential benefit of *Cladomyrma* association to a host is mainly determined by a general difficulty to defend young developing tissue (no matter whether resources are in rich or short supply), we then should expect a similar pattern of biotic defence mechanisms in a wide set of host plants irrespective of their ecological heterogeneity.

The question of how ant-specific traits influence plant defence strategies in ant-plant mutualism is mostly open. More complete information on differences in biotic defence mechanisms among *Cladomyrma* species, paired with data on the temporal and spatial distribution of chemical/mechanical defences in host plants, might offer rewarding avenues to assess if protective ant-plant interactions can deepen our understanding of plant defence in general.

10. Pruning of neighbouring plants

10.1. INTRODUCTION

Several specialised plant-dwelling ants are known to cut back vines and foliage of neighbouring plants that touch the stem or crown of their host (e.g., *Allomerus*: DAVIDSON, LONGINO & SNELLING 1988; *Azteca*: BARNWELL 1967, SCHUPP 1986; *Camponotus*: FEDERLE, MASCHWITZ & FIALA 1998b; *Crematogaster*: FIALA et al. 1989, MASCHWITZ & FIALA 1995, FEDERLE, MASCHWITZ & HÖLLDOBLER 2002, HEIL et al. 2004b; *Pachycondyla*: DAVIDSON & FISHER 1991; *Pheidole*: RISCH et al. 1977; *Pseudomyrmex*: FONSECA 1994, KAMMESHEIDT 1999; *Tetraponera*: YUMOTO & MARUHASHI 1999). Although 'pruning' is usually performed when an alien plant comes in direct physical contact with the ant's host, a few species even attack and destroy any foreign vegetation that grows within a certain distance of the host's trunk, a behaviour that may also be termed 'weeding' or 'clearing' behaviour (*Myrmelachista*: MORAWETZ, HENZL & WALLNÖFER 1992, DAVIDSON & MCKEY 1993b, RENNER & RICKLEFS 1998, OLESEN et al. 2002; *Pseudomyrmex*: ULE 1905, JANZEN 1966 and 1967, LARRERA-ALCAZAR & SIMONETTI 2007; *Tetraponera*: KOHL 1909, JANZEN 1972).

Originally, two main effects of the pruning action have been put forward: (i) it either promotes growth or survival of the host plant by reducing competition for light (in wet forests) or fire risks (in dry forests) and hence indirectly benefits the resident ants (JANZEN 1967) or (ii) it removes bridges over which alien ants can attack the resident colony. The "bridge-demolition" or "ant-invasion" hypothesis (DAVIDSON, LONGINO & SNELLING 1988) is strengthened by the observation that pruning behaviour occurs at a distinctly higher frequency in ant subfamilies with a functional sting than in those with chemical defences, which may generally convey an advantage in aggressive encounters among ants. Although even a single stinging ant may deter a vertebrate, sting defences may be generally inferior to chemical defences in ant-ant conflicts because chemical repellents or insecticides can be applied externally onto the body surface of an enemy, whereas the successful deployment of a sting against rapidly moving or hard sclerotized opponents is much more difficult (e.g., MASCHWITZ 1975). In other words, pruning might have evolved in weakly competitive plant-ants to reduce the threat of invasion by potentially dangerous alien ants. Recent studies support the hypothesis that 'selfish' defence against invasions is a major selective pressure that has led to the development and maintenance of pruning behaviour (SUAREZ, DE MORAES & IPPOLITO 1998, FEDERLE, MASCHWITZ & HÖLLDOBLER 2002, PALMER, YOUNG & STANTON 2002).

Moreover, recent work has shown that certain plant-ants prune and 'castrate' their own host trees (e.g., GAUME, ZACHARIAS & BORGES 2005), thus the general validity of the hypothesis that pruning serves as a protection of the host against plant overgrowth is further weakened. Several explanations have been proposed for this 'parasitic' behaviour in otherwise mutualistic ant partners: (i) it minimises contact with dominant ants occupying neighbouring trees (YOUNG, STUBBLEFIELD & ISBELL 1997, STANTON et al. 1999), (ii) it reduces intraspecific competition between incipient colonies (YUMOTO & MARUHASHI 1999), (iii) it forces the host plant to provide more domatium space (YU & PIERCE 1998, IZZO & VASCONCELOS 2002), or (iv) it is the result of a mismatch between associated ants and plants in which the partners differ in their onset of reproduction (MOOG 2002, MOOG, FIALA & MASCHWITZ 2003). Basically, pruning is employed here in two different contexts: (a) resource allocation – a trade-off between host plant reproduction and domatia space (or nutrition) for resident ants, and (b) competition – a defensive behaviour allowing the coexistence of subdominant plant-ants in the presence of strongly competitive ants.

According to these considerations several traits of *Cladomyrma* appear to make the existence of pruning behaviour in this plant-ant genus less likely. First, *Cladomyrma* is a formicine having chemical defences, hence is thought to have an advantage over ants relying on a sting in aggressive encounters. However, pruning may be directed against other ants with chemical defences. Second, onset of reproduction in *Cladomyrma* occurs relatively early in the ontogeny of the associations. No cases are known in which host plants regularly reach their reproductive stage prior to that of *Cladomyrma*. Third, and most importantly, some *Cladomyrma* species specifically colonise woody climbers as hosts (*Callerya*, *Luvunga*, *Spatholobus*, *Strychnos* and *Sphenodesme*). These hosts are in direct, constant physical contact with supporting trees, thus pruning in climber-inhabiting plant-ants appears to be an absurd, Sisyphean task. To my knowledge, pruning has never been reported in any plant-ant inhabiting woody climbers or climbing palms.

I assume that our understanding of the distribution and extent of pruning behaviour in plant-ants both among taxonomic groups and between biogeographic regions is incomplete. So far, no data have been available about the occurrence of pruning in *Cladomyrma*, one of the most abundant plant-ants in Southeast Asia. Therefore, two basic questions were addressed by this study: Does pruning occur in the genus *Cladomyrma*? Is pruning activity restricted to *Cladomyrma* species inhabiting non-climbing host plants?

10.2. MATERIAL AND METHODS

Study sites and species investigated

Field observations and experiments were conducted at different sites in West-Malaysia and Borneo (Sabah and Sarawak), specifically at the Field Studies Centre in the Ulu Gombak Forest Reserve (3°19'N, 101°45'E), Selangor, in the Kinabalu National Park, substation Poring Hot Springs (6°02'N, 116°42'E), Sabah, and in the Lambir Hills National Park (4°20'N, 113°50'E), Sarawak. Information about the sites and climate is provided in MEDWAY (1972) and DAVIS, HEYWOOD & HAMILTON (1995).

Four *Cladomyrma* species were chosen whose host plants represent different growth forms (Tab. 10-1). Trees: *Cladomyrma maschwitzi* inhabits *Crypteronia griffithii* (Crypteroniaceae), *C. yongi* colonises *Drypetes longifolia* (traditionally placed in the Euphorbiaceae but recently transferred to a new family, Putranjivaceae), *C. dianeae* lives in the domatia of *Neonauclea gigantea* (Rubiaceae), and *C. petalae* is an inhabitant of *Ryparosa fasciculata* (Achariaceae, formerly assigned to the Flacourtiaceae) and *Saraca thaipingensis* (Fabaceae). Climbers: *C. petalae* is notably catholic in its host plant choice and, in addition to the trees *Ryparosa* and *Saraca*, colonises sympatrically the woody climbers *Strychnos vanprukii* (Loganiaceae), *Spatholobus bracteolatus* (Fabaceae) and *Luvunga* sp. (Rutaceae), of which the latter two were included in this study. For details on *Cladomyrma* species and their respective host plant range see AGOSTI, MOOG & MASCHWITZ (1999).

Pruning experiments

To test if *Cladomyrma* ants would attack foreign vines encroaching the stem of their hosts, I first planted the common, fast-growing vine, *Mikania cordata* (Burm. f.) B. L. Robins. (Asteraceae), in plastic bags and tied each bag to a pole. Each pole was placed close to a host plant of *Cladomyrma*, taking care that the pole and the introduced *Mikania* plant did not touch the host plant. Then, one shoot of the *Mikania* vine was carefully twined around a host plant's stem with a pair of tweezers, without using any material to attach the shoot onto the host. This procedure was followed in order to eliminate effects both from stem vibrations of the host plant and contamination of the introduced vine with human odour or foreign objects that may cause alarm recruitment of the ants. The *Mikania* shoots placed in contact with host plants of *Cladomyrma* were roughly classified according to their age: *young* shoots were bright green, soft and flexible whereas *mature* shoots were more or less hardened and had lost their flexibilty to a certain extent (see below).

In each case I selected the contact area of the foreign shoot and the host plant to be within the upper third of a given stem. It is an area where ant patrolling usually occurs at least once or several times a day (*Cladomyrma* ants strongly prefer to patrol on newly emerged internodes and leaf flushes). First, I censused the number of ants within the contact area prior to imposing the treatment, and then monitored the number of ants at, or on, the alien vine at 15, 30, and 90 min intervals after the start of the experiment. After 24 hours I carefully examined each shoot and its associated leaves and leaf petioles for any signs of bites, necrosis or wilting.

Table 10-1: Treatment groups of the pruning experiment with *Mikania cordata* vines. For some colonies more than one experiment was performed; in these cases at least 4 days elapsed before the next trial.

Cladomyrma (*n* colonies tested)	host plant	*n Mikania* young shoots	*n Mikania* mature shoots
	trees:		
dianeae (6)	*Neonauclea gigantea*	6	2
maschwitzi (6)	*Crypteronia griffithii*	6	4
petalae (3)	*Ryparosa fasciculata*	5	2
petalae (6)	*Saraca thaipingensis*	6	0
yongi (6)	*Drypetes longifolia*	6	2
	climbers:		
petalae (2)	*Luvunga* sp.	4	2
petalae (4)	*Spatholobus bracteolatus*	6	1
	∑	39	13

10.3. RESULTS

In all *Cladomyrma* species tested the experimentally introduced *Mikania cordata* shoots caused a significant increase in ant activity within the contact area shortly after start of the experiment. Fig. 10-1 shows the increase in ant number for the pooled data (Friedman test, chi square = 54.237, $df = 3$, $P < 0.0001$, n = 52). The increase in ant activity was observed in both age classes of the *Mikania* shoots but it was more pronounced in the young shoots: $P_{young} < 0.0001$, n = 39, and $P_{mature} = 0.0235$, n = 13 (Friedman test).

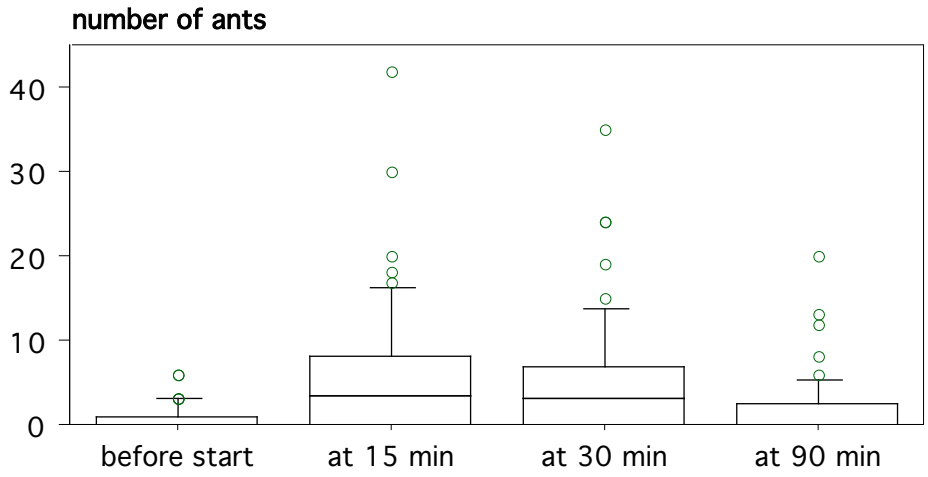


Figure 10-1: Effect of introduction of *Mikania* vines on ant activity of *Cladomyrma* spp. Number of workers at or on the alien vine was recorded at 15, 30, and 90 min after start of the experiment. All data pooled (n = 52). [For explanation of box-whisker plots see figure 4-45.]

Irrespective of the type of host plant (climber or tree), all *Cladomyrma* species tested showed the capability to prune: *C. dianeae* attacked 87.5% (7/8) of the *Mikania* shoots; *C. maschwitzi* 90% (9/10); *C. petalae* 88.5% (23/26); and *C. yongi* 87.5% (7/8). Across all species (data pooled) the shoots were attacked in 88.5% of all replicates (46/52). However, it immediately became apparent that pruning response was negatively correlated with the age (or hardiness) of the introduced shoots (Tab. 10-2). Whereas 95% of all shoots classified as young were attacked (37/39), only 69% of the mature shoots showed signs of bites (9/13). This differences in attack proportion between young and mature shoots is significant (Fisher's exact test, chi square = 6.280, *df* = 1, *P* = 0.0286). Bites on mature shoots, though visible, usually did not reach the vascular bundles and, as a rule, scratched only the bark. In contrast, attacks on a given young shoot usually included at least some bites reaching the vascular bundles. When superficial bite damages are omitted, the proportion of mature *Mikania* shoots attacked is reduced to 23% (3/13).

This result is corroborated when both wilting shoot apices and attacked leaf petioles are considered. Wilting apices amounted to 85% (33/39) in young, and 15% (2/13) in mature shoots (Fisher's exact test, chi square 21.237, *df* = 1, *P* < 0.0001), whereas attacks on leaf petioles were observed in 49% (19/39) of young and 23% of mature *Mikania* shoots (3/13). Although the difference in leaf petiole attacks between young and mature *Mikania* was not significant (Fisher's exact test, chi square = 2.626, *df* = 1, *P* = 0.194), the trend is still visible. Overall, young *Mikania* vines were more strongly affected by pruning than mature vines in the 24 h study period.

Table 10-2: Fate of *Mikania* shoots experimentally placed in contact with inhabited host plants of *Cladomyrma* spp. after 24 hours. Shoot attacked = visible signs of attack after 24 h; shoot not attacked = no visible signs of attack after 24h. Asterisks * indicate superficial bites scratching the bark of the shoot but not reaching the vascular bundles. The sum given in parentheses is the number of mature shoots seriously attacked (superficial attacks omitted).

		shoot		
ant / plant taxa	shoot age	attacked	not attacked	apex wilted
dianeae / Neonauclea	young	6	0	6
maschwitzi / Crypteronia	young	6	0	6
petalae / Luvunga	young	4	0	3
petalae / Ryparosa	young	5	0	4
petalae / Saraca	young	5	1	4
petalae / Spatholobus	young	6	0	6
yongi / Drypetes	young	5	1	4
	∑	37	2	33
dianeae / Neonauclea	mature	1*	1	0
maschwitzi / Crypteronia	mature	3	1	2
petalae / Luvunga	mature	1*	1	0
petalae / Ryparosa	mature	2*	0	0
petalae / Spatholobus	mature	0	1	0
yongi / Drypetes	mature	2*	0	0
	∑	9 (3)	4	2

The *Mikania* shoots experimentally twined around host plants of *Cladomyrma* usually touched the stem only at few contact points. These spots were the preferred areas of attack by *Cladomyrma* workers. The workers chewing on alien shoots were usually found at, or very close to, the contact spot (1–2 cm) with the host stem (Fig. 10-3A). Only *C*. *maschwitzi* workers appear to differ from this pattern (see below). Additional areas of attack were the leaf petiole and, rarely, the leaf lamina (Fig. 10-3C, D).

Figure 10-2 provides the mean percentage of *Mikania* shoots damaged at contact spots by *Cladomyrma*, according to type of damage, i.e. 'bites' and 'necrosis'. Again, the difference between young and mature *Mikania* shoots becomes apparent (Mann-Whitney U-test; for 'bites': $z = 3.342$, $P = 0.0008$; for 'necrosis': $z = 4.513$, $P < 0.0001$). Mature shoots are thus consistently less damaged by *Cladomyrma* during the short-term study period (24 h).

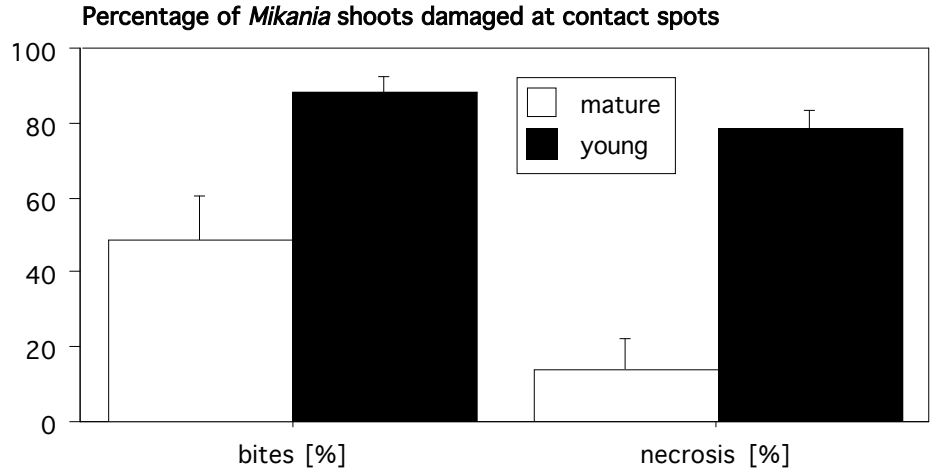


Figure 10-2: Comparison of the mean percentage of damaged *Mikania* shoots at contact spots according to shoot age (young, mature) and damage type (bites, necrosis). Data from four *Cladomyrma* species pooled. Error bars refer to 1 SE.

Although the study was not designed to test for gradual differences between species, the ant *Cladomyrma maschwitzi* appears to differ from all other species tested in several respects. First, mature *Mikania* shoots regularly suffered from attacks by *C. maschwitzi* (in 3 of 4 trials; Tab. 10-2). In the only case where mature shoots were not pruned, the colony showed no activity at all on the plant surface during the study period, suggesting that lack of pruning was a side effect of an unknown cause affecting ant activity in general. Second, intensity of attack against mature shoots was much more pronounced in *C. maschwitzi*. Whereas the other *Cladomyrma* species tested produced only superficial wounds on mature vines during the 24-h interval, the workers of *C. maschwitzi* caused necrosis at least in some of the attacked spots during the study period. Third, the workers of *C. maschwitzi* attacked the *Mikania* not only in the contact area but expanded their pruning area along the *Mikania* shoot up to 10-30 centimetres (Fig. 10-3B).

Under natural, unmanipulated conditions *C. maschwitzi* was observed to prune plants, i.e., an *Uncaria* climber (Rubiaceae), one unidentified vine, and a ginger plant (Zingiberaceae) that came into contact with their host. The workers attacked shoots, tendrils (*Uncaria*), leaf laminae and leaf rachis (ginger), and followed up the alien shoots for 0.3–0.8 meters. However, the ants were never observed to leave their host over the ground to reach neighbouring plants. This is also the case for the other *Cladomyrma* species which restrict their activities to their host.

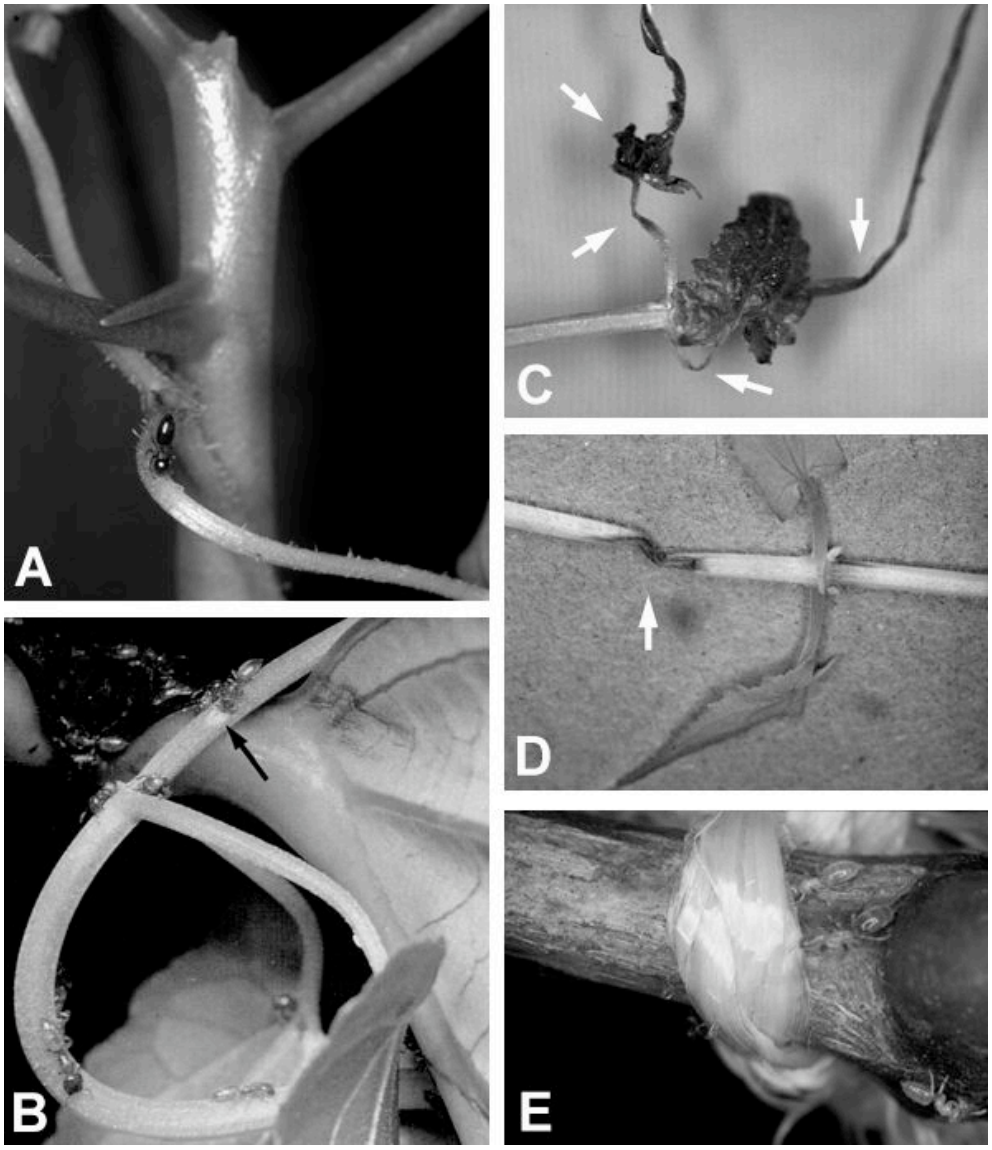


Figure 10-3: Pruning in *Cladomyrma*. **A**: worker of *C. petalae* biting into a *Mikania* shoot touching *Luvunga* host plant; **B**: *C. maschwitzi* ants, inhabiting *Crypteronia*, prune a *Mikania* shoot (arrow indicates wound caused by gnawing); **C** and **D**: effects of pruning at *Mikania* shoots after 24-h (arrows indicate necrosis, wilted apices, damaged leaf petioles and leaf lamina); **E**: *C. maschwitzi* workers attack cord tied to a *Crypteronia* host plant.

Pruning under natural conditions has also been observed once in the second *Cladomyrma* species, *C. crypteroniae*, inhabiting *Crypteronia griffithii*. For the remaining 6 species of the genus not included in this study (*C. andrei*, *C. aurochaetae*, *C. hewittii*, *C. hobbyi*, *C. maryatiae*, *C. nudidorsalis*) the capability to prune encroaching vegetation has yet to be tested. Nevertheless, in three of these remainders, i.e., *andrei*, *hobbyi* and *nudidorsalis*, the ants were seen to gnaw on paper tape used to mark host plants. A similar behaviour was observed in *C. maschwitzi*. The workers attacked a cord tied around a twig (Fig. 10-3E).

Interestingly, at least one *Cladomyrma* species, *C. maschwitzi*, employs chemical 'warfare' against alien shoots by spraying chemical compounds (formic acid) into the wounds after biting, thus promoting necrosis and subsequent wilting of the attacked shoots. A detailed analysis of this behaviour is in preparation (MASCHWITZ, DUMPERT & MOOG).

10.3.1. Summary of the results: pruning behaviour

- ant activity in all *Cladomyrma* species tested (*dianeae*, *maschwitzi*, *petalae*, *yongi*) increased shortly after *Mikania* vines were experimentally twined around the host plant
- within the short-term study period (24-h) pruning signs were observed in all species tested, despite some variability in pruning intensity among colonies and/or species
- across all species, pruning intensity was significantly stronger against young, soft *Mikania* shoots than against mature, harder ones
- attacked shoots or leaf petioles usually developed necrotic areas, often leading to wilting apices or leaves
- pruning behaviour was displayed by both tree- and climber-inhabiting *Cladomyrma* species
- pruning is restricted to alien plants touching the host plant. The ants do not leave their host over the ground to reach and 'weed' neighbouring plants
- other *Cladomyrma* species not included in this study are probably also capable of pruning encroaching vegetation
- preliminary observations suggest that *Cladomyrma* workers, at least of *C. maschwitzi*, use chemical compounds to promote necrosis of attacked shoots

10.4. DISCUSSION

Pruning is part of the behavioural repertoire of many specialised plant-ants. This is the first study to show that species of *Cladomyrma*, one of the largest group of plant-ants in SE Asia, also possess 'horticultural skills'. All *Cladomyrma* species tested attack and prune alien plant parts coming into contact with their host. Already after 24 hours most of the tender *Mikania* vines experimentally twined around the host stem showed signs of bite attacks and necrotic spots causing leaves and apices to wilt. As a rule, *Cladomyrma* species chew the vines only at the contact points with the host, a behaviour also reported for *Azteca* ants inhabiting *Cecropia* (JANZEN 1969a). Although most *Cladomyrma* species investigated restrict their pruning activities to the vine parts in direct physical contact with the host plant, *Cladomyrma maschwitzi* ants may extend their pruning range onto the alien vine for some distance. They do not, however, move down to the ground to reach and attack neighbouring plants to produce a circle of bare ground around their host. Such a 'weeding' or 'clearing' behaviour is known from several plant-ant species from the genera *Myrmelachista*, *Pseudomyrmex*, and *Tetraponera* (ULE 1905, KOHL 1909, MORAWETZ, HENZL & WALLNÖFER 1992, JANZEN 1966, 1967, 1972), but is absent in *Cladomyrma*.

10.4.1. Pruning intensity and climber toughness or age

Several factors are known to cause intraspecific variation in the pruning intensity of plant-ants: (i) morphological properties, e.g. pubescence, of the climber (JANZEN 1967, p. 444), (ii) morphological traits of the host plant –such as waxy or non-waxy stems or presence of ant-attracting extrafloral nectaries– which can be linked to a variable vulnerability to aggressive displacement by enemy ants or competitors (FEDERLE, MASCHWITZ & HÖLLDOBLER 2002, PALMER, YOUNG & STANTON 2002), (iii) presence of enemy ants on neighbouring plants (DAVIDSON 1988, STANTON et al. 1999), (iv) colony size or ant density (JANZEN 1969a, FEDERLE, MASCHWITZ & HÖLLDOBLER 2002), (v) contact point of host plant and climber, i.e., higher pruning level in the host's canopy or at shoots tips (JANZEN 1969a, FEDERLE, MASCHWITZ & HÖLLDOBLER 2002), and (vi) reproductive state of the ant colony (MOOG 2002).

Pruning response to alien plants of all *Cladomyrma* species investigated was biased towards young, soft vine shoots. Pruning intensity was much less pronounced against harder, mature shoots. This difference was independent of other possible sources of variation because the results are based on within-colony tests (mature and young *Mikania* shoots tested on the same colony). In addition, my experiments were performed in the absence of enemy ants. To my knowledge, variation in the intensity of pruning has only once been related to the age or hardiness of the attached climber

shoot. JANZEN (1969a, p. 151) reported that old established vines on *Cecropia* trees occupied by their *Azteca* partner ants are not attacked but show little new growth; when a new tendril or shoot tip came in contact with a *Cecropia* it was neatly trimmed off by the *Azteca* ants along its margin of contact with the host tree. Though not explicitely stated in other studies on pruning behaviour, I suggest that it is generally difficult for plant-ants to kill or remove older vines due to their increased toughness.

Cladomyrma workers prune hard shoots generally more weakly than soft shoots on a short-term basis, however, a long-term study may reveal a stronger effect of pruning against mature shoots. Two observations appear to speak both in favour of this assumption and against it. First, paper tape wrapped around the stem was chewed by all *Cladomyrma* species investigated over a period of one to three weeks until a considerable amount of the material was removed (not tested in *C. aurochaetae*, *C. hewittii*, and *C. maryatiae*). The ants apparently treated the paper strips in the same way as natural vine shoots, indicating that pruning of foreign artificial material may generally be a reasonable estimate of pruning intensity. On the other hand, it is not uncommon to find large and occupied *Cladomyrma* host trees infested with older vine stems and I never observed attacks against established climbers under natural conditions (except in *Crypteronia griffithii* inhabited by *Cladomyrma maschwitzi*). This suggests that ant aggressiveness against foreign older plant parts touching the host may decrease with time, e.g., due to some sort of 'habituation'.

The latter is supported by preliminary observations on mature woody climbers (2x *Uncaria*, 2x unidentified, 1x *Strychnos* sp.) experimentally placed in contact with the host species *Neonauclea gigantea* (n=2), *Drypetes longifolia* (n=2), and *Ryparosa fasciculata* (n=1). In all cases the ants attacked the climbers' stem and produced a few superficial wounds during the first two days. [Note that the stem sections attached to the host did not bear leaves or buds.] Nevertheless, examinations of the climbers after three to four weeks did not reveal any further damage and patrolling workers coming close to the contact area with the climber at the host's stem appeared to 'ignore' the foreign plant, though they usually avoided to walk onto the climber.

It is thus suggested that pruning intensity of *Cladomyrma* is a gradual behavioural response: new growth of alien plants is effectively attacked and killed whereas older shoots suffer less from *Cladomyrma* attack; but a lower level of ant pruning may be effective against climbers when acting over a longer period of time. If climbers manage to get established on the host, *Cladomyrma* workers appear to get accustomed to its presence but pruning of new growth within the contact area with the

host may still occur. Detailed studies are needed to further assess the gradual level of pruning in relation to climber age or toughness.

10.4.2. The *Cladomyrma maschwitzi* case

Among the species investigated, *C. maschwitzi* stands out by its higher pruning intensity (at least against mature shoots) and its wider pruning range. Hypotheses to explain why *C. maschwitzi* differs from the remaining *Cladomyrma* species with respect to pruning behaviour can be grouped into two types based on the advantages pruning confers to the ant and/or to the host.

First, pruning protects the host plant from overgrowth (light competition) and increased pruning activity by *C. maschwitzi* may be an adaptation that enhances mutualistic interactions with the host plant. In symbiotic mutualisms, fitness of the plant-ant colony is tightly linked to survival and growth of the host plant, thus a direct selective advantage of pruning for the plant-ant colony is not required to induce ants to prune. *C. maschwitzi* seems to be most set aside from the other *Cladomyrma* species when the following traits are considered: its host range is restricted to one single plant taxon and it is also the most widely distributed *Cladomyrma* species. These traits combined probably suggest that the mutualism between *C. maschwitzi* and *Crypteronia griffithii* is the oldest (and most advanced?) among the *Cladomyrma* / plant associations.

The second type of hypothesis is that the increased pruning activity of *C. maschwitzi* is linked to a direct benefit to the ant colony. A growing body of evidence supports the idea that pruning behaviour observed in plant/ant systems has arisen as a means of reducing the threat of invasions by enemy ants (DAVIDSON, LONGINO & SNELLING 1988, FEDERLE, MASCHWITZ & HÖLLDOBLER 2002). Furthermore, in some systems pruning by plant-ants appears to have such a strong 'selfish' component that it leads to the damage of the host plant (YU & PIERCE 1998, IZZO & VASCONCELOS 2002, MOOG 2002, PALMER, YOUNG & STANTON 2002). Several explanations have been proposed for this 'parasitic' behaviour in otherwise mutualistic ant partners (see Introduction). [However, the plausible notion that pruning of the own host plant is simply an extension of the pruning activities directed to alien plants remains to be tested.] Generally, these findings indicate that the role of persistence (e.g., the ability to resist invasion) as a strategy of plant-ants to coexist with competing or predatory ant species has been underestimated in earlier studies.

Among *Cladomyrma* species, *C. maschwitzi* is certainly one of the most timid ants. It is also one of the smallest species of the genus (AGOSTI, MOOG & MASCHWITZ 1999). Although comparative data on competitive ability are lacking, *C. maschwitzi* appears

to be a weak competitor in ant-ant encounters compared to most other *Cladomyrma* species. This emphasises the possible significance pruning has for *C. maschwitzi* to keep their host free of contact points with neighbouring plants, hence reducing the threat of invasion by potentially dangerous ants. Moreover, all host plants of *Cladomyrma* lack physical barriers such as trichomes and waxy, 'slippery' stems that have been described to help plant-ants to persist on their host (DAVIDSON, SNELLING & LONGINO 1989, FEDERLE et al. 1997). That such morphological plant traits can be directly linked to the intensity of pruning has been demonstrated by FEDERLE, MASCHWITZ & HÖLLDOBLER (2002). Pruning intensity of *Crematogaster* species inhabiting *Macaranga* trees having glaucous stems was less pronounced than in those inhabiting non-glaucous *Macaranga* hosts.

Differences in pruning activity have also been reported for *Myrmelachista* plant-ant species occupying *Ocotea* trees in Central America (DAVIDSON & MCKEY 1993b). Here, some *Myrmelachista* species do prune whereas others do not. In Central Amazonia, ants of this genus not only prune, but maintain vegetation-free zones around their host plants, all trichome myrmecophytes (*Cordia*, *Duroia*, *Tococa*). The authors suggest that increasing specialisation and host specificity of *Myrmelachista* might be paralleled by a weakening competitive ability, the latter probably explaining the differences in pruning among *Myrmelachista* plant-ant species. A phylogenetic analysis of the genus *Cladomyrma*, paired with complete information on pruning behaviours and competitive abilities for all *Cladomyrma* species, would help to discern whether or not such a scenario holds for *Cladomyrma* as well.

10.4.3. Pruning in climber-inhabiting *Cladomyrma* species

Worldwide, only a very small number of myrmecophytic plant taxa show growth forms as climbers: myrmecophilous or myrmecophytic species from several genera of rattan-palms form the dominant group, i.e., *Calamus*, *Daemonorops*, *Eremospatha*, *Korthalsia*, *Laccosperma*, *Oncocalamus*, and *Pogonotium* (DRANSFIELD & MANOKARAN 1994, SUNDERLAND 2002). Less well-known ant-associated climbers are found in the genera *Canthium*, *Capparis*, *Dichapetalum*, *Ficus*, *Poikilospermum*, *Vitex*, *Uncaria*, and *Wightia* (DAVIDSON & MCKEY 1993, MASCHWITZ et al. 1994b and 1996a, JOLIVET 1996, MOOG et al. 2003). Pruning has never been reported for ants in association with one of these taxa.

Members of the genus *Cladomyrma* are remarkable in forming association with woody climbers. Four *Cladomyrma* species (*andrei*, *hobbyi*, *petalae,* undet.) are known to inhabit six liana species in five genera (*Callerya*, *Luvunga*, *Spatholobus*, *Strychnos* and *Sphenodesme*). *Cladomyrma* is thus the predominant coloniser of woody climbers

worldwide, only rivalled by several *Camponotus* (subgenus *Myrmoplatys*) species which are obligate ant partners of myrmecophytic rattans in SE Asia (WERNER 1993). Recently, the response of *Myrmoplatys* sp. to alien vines infesting the host *Korthalsia robusta* was tested in Borneo. According to U. MASCHWITZ (pers. communication), this *Myrmoplatys* species does not prune encroaching vines.

In contrast to *Myrmoplatys* and other climber-inhabiting plant-ants, this study demonstrated that pruning is part of the behavioural repertoire of *Cladomyrma petalae*, a species inhabiting the woody climbers *Luvunga* sp., *Spatholobus bracteolatus*, and *Strychnos vanprukii*. However, because climbing host plants are in direct, constant physical contact with supporting trees, it seems highly unlikely that climber-inhabiting plant-ants generally attack any foreign plant parts. How can this apparent contradiction be explained?

Two types of hypotheses might apply to this striking phenomenon. First, *Cladomyrma petalae* ants do not indiscriminately attack any alien plant part, rather they select foreign plant tissue soft enough to being mauled or, for example, they rapidly lose interest in non-host plant tissue if pruning of hard shoots would require a high energy investment. And indeed, *Cladomyrma* species (incl. *C. petalae*) generally display a significant higher level of pruning intensity against young, soft shoots than against mature ones. The problem with this explanation is that it is not clear why ants inhabiting climbing host plants should prune at all. If the principal selective advantage of this behaviour is to reduce the threat of invasions by more dominant competing and/or predatory ants, then the probability of encounters with enemy ants remains relatively high because the latter can enter the climbing host plant easily and in masses by the numerous contact points with the supporting tree (phorophyte). However, pruning of new growth of the phorophyte near the attached host climber may still confer a benefit to the plant-ant colony because it reduces the number of contact points to a level which allows an effective defence of the host and/or it reduces the opportunities for alien ants to establish feeding sites with trophobiotic insects on new leaves and shoots in close vicinity to the plant-ant colony. [Sites of ant–trophobiont aggregations are usually found on fresh plant growth (e.g., BLÜTHGEN & FIEDLER 2002, DILL, WILLIAMS & MASCHWITZ 2002).] If, on the other hand, the major advantage of pruning is to free the host plant from light competition, pruning of the phorophyte may promote growth of the host climber and, in turn, may increase nesting space for the inhabiting ants. Whatever the principal advantage of pruning might be, this type of hypothesis predicts that pruning by a climber-inhabiting plant-ant confers a direct or indirect benefit to the ant colony or the host plant.

The second type of hypothesis is that pruning confers no particular advantage to the climbing host plant or the associated plant-ant, but (i) simply reflects an ancestral character of the plant-ant species or (ii) is maintained because the plant-ant sympatrically colonises several host plants of different growth forms (trees and climbers). The latter is a striking trait in *Cladomyrma petalae*. With six different host plant taxa the range of environments inhabited by *C. petalae* is the most heterogeneous among *Cladomyrma* species. The host range includes three trees (*Drypetes*, *Ryparosa*, *Saraca*) and three climbers (*Luvunga*, *Spatholobus*, *Strychnos*). Thus, pruning might convey a direct benefit to *C. petalae* when inhabiting a tree as it removes contact points to the neighbouring vegetation where invasions of enemy ants could occur. Preliminary experiments on host selection by *C. petalae* (see chapter 5) indicate that alate females from populations living in the tree *Saraca* accept the climbers *Strychnos* and *Spatholobus* as hosts for colony-founding (and vice versa). This suggests that gene flow between populations of *C. petalae* inhabiting different host taxa may be relatively high and, in consequence, pruning as a possibly beneficial behavioural trait of *C. petalae* in part of its environments (tree hosts) is maintained throughout the host range.

The alternative explanation, i.e., pruning confers no advantage to *C. petalae* and is an ancestral trait retained by some form of 'phylogenetic inertia', does not appear to be a more plausible explanation. Although pruning is probably a plesiomorphic character shared by all members of the genus *Cladomyrma*, there is no evidence why pruning should have lost its significance in *C. petalae*. This species displays the typical set of plant-ant traits seen in other *Cladomyrma* species, e.g., efficient host selection, early colonisation of juvenile plants, host fidelity, activity pattern ('neophily'), cleaning behaviour and protection against herbivorous insects. In addition, *C. petalae* strongly competes for nesting space with several (non-pruning) *Crematogaster* species which facultatively nest in host plants of *Cladomyrma* (MOOG 1991, RIEDEL 1997). Although the strong colonisation ability of *C. petalae* produces a 'priority effect', they may secondarily be displaced by *Crematogaster* species. In staged encounters between similar-sized colonies of a certain *Crematogaster* species (sp. 1) and *C. petalae*, the latter successfully defended its host plant against invasion by *Crematogaster* ants (n=5; unpublished results), showing that established colonies of *C. petalae* are strong competitors. However, when the colony size of *C. petalae* was distinctly smaller (about half the size) than that of *Crematogaster* sp. 1, the *Cladomyrma* colony was evicted and killed (n=6). This suggests that pruning by *C. petalae* during at least a part of the colony's ontogeny might effectively enhance the ability to resist invasion by enemy ants.

With respect to pruning, *C. petalae* cannot be compared with the two other *Cladomyrma* species known to colonise climbing host plants due to lack of data. In Borneo, *C. andrei* and *C. hobbyi* inhabit the woody climbers *Callerya nieuwenhuisii* and *Spatholobus oblongifolius*. Whereas *C. hobbyi* has been collected from *Spatholobus oblongifolius* only, *C. andrei* has been found on both liana species as well as on the Bornean form of the tree *Drypetes longifolia*. Both ant species were observed to gnaw on paper tape used to mark host plants, suggesting that they are capable of pruning. However, climber-inhabiting plant-ants are expected to possess a certain degree of competitive ability in ant-ant conflicts (as seen in *C. petalae*) to facilitate persistence on their host plants. Because experimental work on pruning behaviour among *Cladomyrma* species is incomplete, and because a phylogenetic analysis of the genus is lacking, it cannot be discerned from available evidence whether pruning by climber-inhabiting *Cladomyrma* is advantageous in their respective environments (and may be advantageous to the plant as well) or whether its maintenance is simply due to host plant heterogeneity (in terms of growth form) or to some form of 'phylogenetic inertia'.

10.4.4. Chemical 'warfare'

Preliminary data indicate that *C. maschwitzi*, and probably some other *Cladomyrma* species, spray chemical compounds (formic acid) into the wounds inflicted by chewing an alien shoot, thereby promoting necrosis and subsequent wilting of the attacked shoot (MASCHWITZ, DUMPERT & MOOG, in preparation). Chemical 'warfare' by pruning ants is much less well-understood than claimed by previous studies. Here, I briefly summarise the scanty evidence for the existence of such a behaviour.

JANZEN (1969a) viewed pruning plant-ants as 'allelopathic' agents because "they are functionally analogous to the chemicals liberated by some plants in their competitive interactions with other plants." Typically, such ant-mediated allelopathy is achieved by the ants' biting off, and sometimes stinging into, shoots or leaves of foreign plants (JANZEN 1969a, DAVIDSON, LONGINO & SNELLING 1988). JANZEN (l.c.) assumed that stinging of alien vines by *Pseudomyrmex* ants perhaps caused some necrosis, but he had no evidence that *Azteca* plant-ants, lacking a functional sting, release defensive compounds into the plant wounds. The latter case, i.e. the additional deployment of a toxin after biting, has been reported by MORAWETZ, HENZL & WALLNÖFER (1992): *Myrmelachista* ants, inhabiting *Tococa occidentalis*, first bite into the petiole or leaf vein of an alien plant, then turn over and spray a 'herbicide' from their gaster into the wound that causes necrosis and dehiscence, eventually killing the whole plant. The nature of the 'herbicide' has only recently been analysed, it is formic acid (FREDERICKSON, GREENE & GORDON 2005). To my knowledge, the use of formic acid

against vegetation has only once previously been confirmed in the North American mound-building ant *Formica exsectoides* which attempts to kill any vegetation which may grow on the mound or shade the area of the nest (ANDREWS 1928). In the case of trees, the ants first tear away enough of the outer bark to expose the phloem and then flood the exposed area with formic acid. The formic acid causes coagulation of the contents of cells in and around the phloem and sap flow stops, preventing nutrients from moving through the bark, and effectively girdling the tree.

Although it is now indubitable that the vegetation-free zones –the so-called 'devil's gardens'– around host plants of *Myrmelachista* are created by the ants (FREDERICKSON, GREENE & GORDON 2005), the origin of the clear patches has long been controversial. Whereas some authors favoured an allelopathic effect caused by the host plant itself over 'allelopathy' mediated by the *Myrmelachista* ants (CAMPBELL, RICHARDSON & ROSAS 1989, PFANNES & BAIER 2002), others supported the work of MORAWETZ, HENZL & WALLNÖFER (1992) and attributed the observed 'allelopathy' solely to the activity of *Myrmelachista* ants (RENNER & RICKLEFS 1998, OLESEN et al. 2002).

Evidence for allelopathic properties of plant compounds in the ant-plant *Duroia hirsuta* has been reported by CAMPBELL, RICHARDSON & ROSAS (1989), PAGE, MADRINAN & TOWERS (1994), and AQUINO et al. (1999). However, the isolation of various allelopathic compounds out of plant tissues *per se* is not simply comparable with field conditions since many plant compounds have allelopathic effects that are concentration sensitive and dependent on the affected plant. A possible explanation for the above described discrepancy may lie in behavioural differences among *Myrmelachista* species involved in the studied associations. *Myrmelachista* species are known to differ in their capability to prune (DAVIDSON & MCKEY 1993b), however, two studies of the *Myrmelachista / Duroia* association were conducted at the same site (Yasuni NP, Ecuador) and still yielded contrasting results (PFANNES & BAIER 2002, OLESEN et al. 2002). Unfortunately, the identity of the involved *Myrmelachista* species is unresolved and a taxonomic revision of the genus is needed.

This brief review demonstrates the ambiguous nature of the existing knowledge on chemical 'warfare' in pruning ants. Moreover, the use of chemical compounds to foster the efficacy of mechanical pruning has never been reported for most of the rather well-known groups of plant-ants, i.e., *Allomerus* (in *Cordia*), *Azteca* (*Cecropia*), *Crematogaster* (*Macaranga*), *Pheidole* (*Piper*), and *Tetraponera* (*Barteria*). Thus, it cannot be assessed by the available evidence if the deployment of chemical substances during pruning by *Cladomyrma* (at least in *C. maschwitzi*) is a trait shared by plant-ants of

different genera and subfamilies. This hinders a well-founded discussion of the evolutionary origin of this behaviour. Interestingly, a recent morphological analysis, however, provides evidence that Asian *Cladomyrma* is most closely related to New World *Myrmelachista* and *Brachymyrmex* (LAPOLLA & LONGINO 2006). I speculate that chemical 'warfare' by pruning ants mirrors the behaviours seen in these ants involved in combats with alien ants and thus it may simply be an expression of a general aggressiveness deployed in a different context.

11. Concluding discussion

Within the ants a number of lineages have developed exquisitely arboreal habits; they nest entirely within plant cavities and exhibit a specialised morphology and behaviour for doing so (e.g., WARD 1991, FIALA, MASCHWITZ & THO 1991, LONGINO 2006). Species within these lineages often show a range of specialisation, being generalist inhabitants of dead or live stems, or specialist inhabitants of live stems. The latter group is often involved in obligate associations with particular lineages of plants and is particularly important in the study of mutualism, the cooperative interaction between species (BRONSTEIN 1998). Among these stem-nesting ants is the formicine genus *Cladomyrma*. All known species of this group are arboreal, nesting exclusively in live stems. These ants are inconspicuous and have been little studied, but this work has shown that they are far richer and with more complex plant associations than previously suspected.

After the discovery of the first species of the ant genus *Cladomyrma* by W. DOHERTY and its description by EMERY (1894, as *Dimorphomyrmex andrei*) the genus remained virtually unknown to the scientific world. Over the next four decades only two additional species were described in the genus (WHEELER 1910, DONISTHORPE 1937) and their natural history and host plants were still a mystery The discovery of new *Cladomyrma* species some 50 years later by MASCHWITZ et al. (1989, 1991) shed new light on their lifestyle and host affiliations. Recently, the new species collected have been described by AGOSTI, MOOG & MASCHWITZ (1999) and EGUCHI & BUI (2006); currently the genus consists of at least 12 species.

In over 100 genera of tropical angiosperms, one or more species possess specialised structures for housing ants (DAVIDSON & MCKEY 1993a), encouraging more constant and long-lived associations. The longevity and intimacy of these associations has often facilitated an increasing specialisation of both the ants and the plants, leading to a number of highly specific and obligate symbioses. As hypothesised by JANZEN (1966), ants that better protect their host plant, and plants that invest more in maintenance of their resident ants, should thereby increase their own survival and reproduction. Are the associations of *Cladomyrma* with plants true mutualisms?

Interspecific interactions are traditionally displayed along a gradient, placed according to its outcome (negative, neutral or positive) for each partner. BRONSTEIN (1994), however, emphasised that field studies consistently find the costs and benefits that determine net effects to vary greatly in both space and time. For example, outcomes may depend on size or age of one of the participants, or they may vary with the habitat

in which the interactions take place. Other sources for conditional outcomes are the identity and local abundance of the mutualistic partner, herbivore pressure, or exploitation by 'cheaters' (BRONSTEIN 1994, 1998, 2001, and references therein).

In short, the question arises to "when and where is mutualism?" – a direct allusion to JANZEN'S (1980) and THOMSON'S (2003) articles "When is coevolution?" and "When is it mutualism?", respectively. In *Cladomyrma*/plant associations things are probably more complex than they first appear. To begin, I consider the costs and benefits for each partner, the plants and the ants. Although the limited data presently available prevent me from drawing firm conclusions I attempt to define the critical points in the mutualism between *Cladomyrma* and its host plants.

Ant-plant protection mutualisms have also served as model systems for studying aspects of coevolutionary specialisation (JANZEN 1966, FIALA & MASCHWITZ 1992a, WARD 1993, BROUAT et al. 2001, QUEK et al. 2004), plant defence theory (MCKEY 1988a, FONSECA 1994, ANSELLEM & MCKEY 2006, HEIL 2008), the structure of food webs (LETOURNEAU & DYER 1998a+b, MCKEY et al. 2005, DYER 2008), the evolution of allometry in modular organisms (BROUAT & MCKEY 2000) and biogeography (QUEK et al. 2007). In addition, they have figured prominently in recent work on species coexistence (FONSECA & BENSON 2003, PALMER, STANTON & YOUNG 2003, YU et al. 2004, DEBOUT et al. 2009) and the maintenance and stability of mutualisms (YU 2001, IZZO & VASCONCELOS 2002, CLEMENT et al. 2008, PALMER et al. 2008).

The *Cladomyrma*/plant associations provide material for a wide range of questions in ecology and evolutionary biology. Some aspects, for instance plant defence theory and host specialisation (e.g., domatium formation), have already been highlighted in previous chapters (p 150, 270). Here, I will present an overview of the ants' host specificity and its implications for the limits of specialisation. Finally, I propose a scenario in which three key traits are hypothesised to have resulted in *Cladomyrma* conserving the potential to colonise, over evolutionary time, new hosts and creating unique niches. It's suggested that the *Cladomyrma*/plant mutualism provides excellent examples of niche construction thus making unique ecological and evolutionary contributions to tropical diversity.

11.1. A plant's perspective: benefits of being colonised by *Cladomyrma*

This work demonstrates that all species of *Cladomyrma* investigated (*dianeae*, *maschwitzi*, *yongi*, *petalae*) confer antiherbivore protection to young leaves of its host. The ants also attack and repell or kill herbivorous insect larvae encountered on young foliage. At least in one case, the ants seem to discourage female lycaenid butterflies

from egg-laying. Observations also indicate that flying herbivores such as chrysomelid beetles and cicads avoid contact with ant workers and feeding time on host tissue may thus be reduced. In my short-term experiments the protection of young foliage varied considerably among host plants and associated *Cladomyrma* species (see figure 9-9). This is, however, not a direct reflection of differences in the protective efficacy among ant species because young leaves, for example, of ant-free *Saraca* accumulated distinctly greater mean herbivore damage (34%) than those of ant-free *Crypteronia* (12%), indicating that herbivore pressure and/or plant resistance to herbivores differ between host plant species. It would be promising to study the beneficial effect of *Cladomyrma* species inhabiting the same host taxon at the same study site, e.g., *C. maschwitzi* and *C. crypteroniae* on *Crypteronia griffithii*.

Cleaning behaviour appears to be a trait shared by all members of the genus, and the two species tested (*maschwitzi*, *petalae*) successfully removed termite eggs experimentally placed onto young leaves. Another trait common to all known species of the genus is that the ants preferentially patrol young shoots and leaves ('neophily'). These behavioural traits of *Cladomyrma* combined likely reduce stem damage and pathogenic infection of their host but this remains to be elucidated. In the last decade, evidence for protection against fungal pathogens has accumulated (*Cecropia*: BELIN-DEPOUX et al. 1997; *Piper*: LETOURNEAU 1998; *Macaranga*: HEIL et al. 1999, 2001a). Ant-mediated antiherbivore protection is expected to generally reduce leaf fungal infection because the predominant mechanism of fungal establishment in tropical understorey plants is wounding, such as that caused by herbivory (GARCIA-GUZMÁN & DIRZO 2001).

The ants prune encroaching vegetation (tested in *dianeae maschwitzi*, *petalae*, *yongi*, observed in *crypteroniae*) and attack paper tape used to mark host plants (observed in *andrei*, *dianeae*, *hobbyi*, *nudidorsalis*, *maschwitzi*, *yongi*, *petalae*). However, the beneficial effect of pruning to the host plant, e.g. by reducing competition for light, is not clear. The response of *Cladomyrma* to plants encroaching the host stem is highly variable and sometimes inefficient, probably serving another function such as the reduction of 'entry points' for opportunistic ants (see chapter 10). Overall, a protective effect of at least some of the *Cladomyrma* species to their host has been unambiguously demonstrated and the behavioural traits of *Cladomyrma* are compatible with traits exhibited by other protective plant-ants. If this translates into a better reproductive success of the hosts has yet to be verified. Evidence for lifetime fitness benefits is particularly difficult to quantify for the long-lived woody host plants of *Cladomyrma*.

Host plants might also benefit from nutrient uptake through ant faeces or breakdown of collected debris in the ant domiciles. Although the flow of nutrients appears to be principally from the plant to its resident ants, some examples provide evidence that nutrient flow can be reversed, especially in ant-epiphytes living in nutrient-poor habitats (epiphytes: BENZING 1970, HUXLEY 1978, RICKSON 1979, RICO-GRAY et al. 1989, TRESEDER, DAVIDSON & EHLERINGER 1995, WEISSFLOG et al. 1999; *Tococa*: NICKOL 1993 a+b, CABRERA & JAFFE 1994, ALVAREZ et al. 2001; *Maieta*: BELIN-DUPOUX & BASTIEN 2000, SOLANO & DEJEAN 2004; *Piper*: FISCHER et al. 2003; *Cecropia*: SAGERS et al. 2000).

The latter example illustrates the problems associated with generalising about nutrient fluxes in ant-plant mutualisms. SAGERS et al. (2000) studied the relationship between *Cecropia peltata* and an undetermined *Azteca* species in Trinidad, coming to the conclusion that previous studies misjudged the flow of nutrients in *Cecropia-Azteca* mutualisms: although ants consume plant products (specialised food bodies), they provide more nutrients than they receive. However, the identity of the *Azteca* species inhabiting *C. peltata* in Trinidad has not been established and, according to LONGINO (1991a+b, 1996), the different *Azteca* ants differ strongly in their specialisation as plant-ant. Therefore the data presented by SAGERS et al. (2000) may be obtained from an *Azteca* species known as a live stem-dwelling generalist. These ants are generally believed to provide weak protection to their host and to derive a considerable greater portion of their food off the plant, suggesting that the situation in Trinidad –with *Azteca* being in its marginal geographic distribution and *Cecropia* having a relatively low occupancy rate (CYNTHIA SAGERS, pers. comm)– is an aberration rather than the 'typical' case of a *Cecropia-Azteca* mutualism.

There is no evidence that host plants of *Cladomyrma* derive an important part of their nutrients (nitrogen, phosphorus) from their resident ant colony. In the stem cavities very small amounts of debris can be found in more or less regular intervals, recognisable as short sections with blackish inner stem walls (caused by an unidentified fungus). These blackish areas occur in all hosts, irrespective of plant taxon or *Cladomyrma* species, they may be defecation sites of the ants. Recently, workers of the African plant-ant *Petalomyrmex* were observed to chew fungus hyphae in the domatia of their host plant *Leonardoxa* (DEFOSSEZ et al. 2009). The authors provide some evidence that the association between the fungus and the ant may be symbiotic, and they hypothesise that the fungus could be a nutrient recycler decreasing the nitrogen and phosphorus cost of the symbiosis for the plant. Historical records show that occurence of fungi in myrmecophytes appears to be a rather widespread phenomenon (BAILEY 1920, CHODAT & CARISSO 1920, DOCTERS VAN

LEEUWEN 1929a, WHEELER 1942, JANZEN 1972), however, the nature of the fungus and its role in these ant/plant systems remains to be elucidated. In the *Cladomyrma*/plant mutualism, remains of dead ant workers are usually discarded through the exit holes and are not deposited in the nest cavities. In addition, my experiments indicate that herbivores killed on the plant surface are thrown off the plant, rather than transported into the nest. Another potential nutrient source for the host plant, food storage, has not been observed in *Cladomyrma* ants which appear to depend in their diet mainly on hemipteran trophobionts. I also have never observed large piles of debris in hundreds of stems dissected. Nutrient flux from ant to plant thus appears to be of minor importance in the *Cladomyrma*/plant system, as is the case in the *Pheidole*/*Piper* mutualism (FISCHER et al. 2003). Ant-mediated nitrogen uptake by myrmecophytic *Piper fimbriulatum* was calculated to account for less than 1% of the plants' above-ground nitrogen demand.

11.2. A plant's perspective: costs of being colonised by *Cladomyrma*

The maintenance of a protective ant colony imposes costs to the plant if the allocation of limited resources entails negative effects on fitness (HEIL & MCKEY 2003). In myrmecophytic *Macaranga bancana*, for example, food body production by saplings amounted to about 5% of total aboveground biomass production (HEIL et al. 1997). In addition, the production of a higher amount of food bodies by *M. bancana* can increase the size of the partner ant colony, the latter being correlated with defensive efficacy (HEIL et al. 2001b, ITINO et al. 2001b). Food body production of myrmecophytes has been shown to be limited by soil nutrient content (*Macaranga*: HEIL et al. 2002b) and light and nutrient availability (*Cecropia*: FOLGARAIT & DAVIDSON 1994, 1995), indicating that production of food rewards for ants is sensitive to costs.

Ants receive the food rewards either directly via extrafloral nectar (EFN) and food bodies (FB), or indirectly via honeydew of hemipteran trophobionts. A large portion of ant/plant mutualisms have trophobiotic coccoids (Coccidae, Pseudococcidae) as a third partner (DAVIDSON & MCKEY 1993a, MOOG et al. 2003). In the *Cladomyrma*/plant system the coccids and pseudococcids appear to be essential because ants usually do not forage off the host and because most host plants produce no direct food rewards, except *Saraca thaipingensis* (EFN) and possibly *Ryparosa fasciculata* in which FB scars are evident (WEBBER et al. 2007). In both cases, however, ant workers have not been observed to regularly utilise these rewards. Food bodies of myrmecophilic but non-myrmecophytic *Macaranga* species, although collected by a large variety of opportunistic ants, are ignored by *Cladomyrma petalae* workers (FIALA & MASCHWITZ 1992b).

The hidden location of the trophobionts in hollowed stems makes it particularly difficult to determine the kinds and amounts of resources coccoids supply to the ants. Also, the experimental manipulation is almost impossible without dissecting live stems, thereby destroying the feeding substrate of the coccoids. However, *Cladomyrma* ants have actually been observed to take up honeydew droplets from tended coccoids, and several additional observations indicate the particular importance of trophobionts as food supply for *Cladomyrma* ants. Coccoids are acquired early in the ontogeny of a colony and the successful establishment of a colony on a host plant seems to be dependent on the presence of coccoids (chapter 6; MOOG et al. 2005). After damage to the stem, worker ants not only rescue their larvae but also transport their trophobionts into intact stem parts.

It is widely assumed that the feeding of a resident ant colony via hemipteran honeydew is a process over which the plant has no or limited control (HEIL & MCKEY 2003). It should be noted, however, that *Cladomyrma* colonies appear to keep their coccoid population in control. Although the ratio between the number of workers and coccoids is variable (2:1 to 24:1, mean 10.5 ± 5.8 SD; n=58), it is low compared to the 'overcrowded' populations of trophobionts I occasionally observed in hosts overtaken by opportunistic ants. Here the coccoids built a 'carpet' on the domatia walls and, in places, on the stem surface, probably leading to a severe over-exploitation of the host plant. Such mass infestation is absent from *Cladomyrma*/plant associations, and the plant surface is always free of trophobionts. This is indicative of a low but constant and relatively 'predictable' cost without extremes when a plant is colonised by the plant-ant *Cladomyrma*. Similarly, myrmecophytic *Macaranga* plants that are colonised by their specific *Crematogaster* plant-ants are effectively protected from exophytic scale insects (HECKROTH et al. 2004b). In contrast, exophytic non-mutualistic Coccidae caused the death of all infested *Macaranga bancana* seedlings after eight months when the ant partner was excluded.

A study by GAUME, MCKEY & TERRIN (1998) suggest that the third partner in the system, the trophobiont, affects the outcomes of the interaction for the ants and for the plant in different directions. Larger colony size (relative to tree size) translates into greater protection against herbivory; a relationship that appears to be common to the majority of ant/plant associations. In the African *Leonardoxa*/*Aphomomyrmex* mutualism, however, this relationship was more pronounced for trees whose ants tend pseudococcids than for those in which ants tend coccids (GAUME, MCKEY & TERRIN 1998). Second, for trees (and associated ant colonies) of comparable size, biomass of trophobionts was much larger in trees harbouring coccids than in trees with pseudococcids. Thus, the cost to the tree of maintaining ants may be greater when

ants are associated with coccids. In contrast, *Aphomomyrmex* ants gain more in terms of reproductive output in being associated with coccids. The identity of the trophobiotic partner may thus be a source of conflict between the other two partners (HEIL & MCKEY 2003).

There is yet no evidence for a similar potential conflict in *Cladomyrma* systems. First, established colonies of most *Cladomyrma* species tend pseudococcids as their sole trophobiont and, with few exceptions, especially in *C. maschwitzi*, coccids occur only occasionally in small numbers. Second, the taxonomic range of mealybugs associating with *Cladomyrma* (29 species from nine genera) exceeds by far the known range in the *Aphomomyrmex* system (one species), thus adding a considerable degree of complexity. On each host plant a *Cladomyrma* species may associate with a set of available trophobiotic partners and the outcome of the association may be affected differently in each resulting three-partner-system. The dynamics of such mutualistic interactions involving more than a single trio of species depend on the relative costs and benefits of interaction among alternative partners.

The costs to the host plant by the maintenance of an obligate mutualistic ant has an additional often neglected side effect. Because *Cladomyrma* always hollows out the solid stem, nest chambers are provided previously not available for opportunistic arboricolous ants. These nesting opportunities impose the risk of 'overtaking' by facultative ants providing less or no benefits to the host. In fact, such combats between resident *Cladomyrma* and opportunistic *Crematogaster* have been observed occasionally. Secondary colonisation of hollowed-out stem nests may also occur after the 'natural' death of the *Cladomyrma* colony. In any case, species turnover increases the variation in costs and benefits, probably pushing the effect of ant occupancy more towards a point where benefits do not exceed costs.

Food rewards for mutualist ants, such as extrafloral nectaries and food bodies, are predictable and attractive food sources for other ants and arthropods. They may deplete the ant partner's food resources and behave aggressively against or even prey on the plant-ants (DYER & LETOURNEAU 2003). Wasps of the genus *Charterginus* (Epiponini) rob food bodies from myrmecophytic *Cecropia* even in the presence of their *Azteca* mutualists (LAPIERRE, HESPENHEIDE & DEJEAN 2007). However, several ant-plants traits can reduce costs of lost food rewards for mutualists by providing filter mechanism that limit the access to food ressources for nonmutualists. *Macaranga* ant-plants hide food from intruders by slippery wax barriers or by producing food bodies under recurved stipules (FEDERLE & RHEINDT 2005). Access to food resources is most effectively limited when myrmecophytes supply them inside the domatia, so that ant

foraging occurs in seclusion. For example, many plant-ants, including *Cladomyrma*, obtain most of their nutrition from endophytic scale insects, and even food bodies and extrafloral nectaries can be supplied inside the domatia (food bodies, *Piper*: RISCH & RICKSON 1981; *Maieta*: VASCONCELOS, 1991, *Tococa*: ALVAREZ et al. 2001; extrafloral nectaries, *Callicarpa*: JANKA et al. 2000; *Hirtella*: LEROY et al. 2008).

Costs may also arise from specialised herbivores which circumvent the defensive behaviour of the ant mutualist, although few seem to have evolved successful counter-adaptations against plant-ants. In several *Macaranga*/*Crematogaster* mutualisms, for example, specialised lycaenid butterflies of the genus *Arhopala* suppress ant aggressiveness by releasing 'appeasement' substances (MASCHWITZ et al. 1984, FIEDLER 1999). However, *Cladomyrma* has never been observed to tend myrmecophilous lycaenid caterpillars. In contrast, the caterpillars are attacked and killed or removed from the host. Only one lycaenid, the flower-feeding specialist *Jamides caerulus*, is currently known to escape predation by *Cladomyrma* ants through 'concealed feeding', even though the ant workers readily killed all *J. caeruleus* larvae offered during experiments (SEUFERT & FIEDLER 1996). The habit of concealed feeding is probably one important reason why (unidentified) herbivores of *Crypteronia griffithii* and *Spatholobus bracteolatus* survive in the presence of *Cladomyrma* ants (see chapter 9). In Costa Rica parasitism levels of leaf miners were observed to be lower on *Cecropia* trees occupied by more active colonies of *Azteca* (LAPIERRE 2001). Gall-making cecidomyiid flies sometimes infest the leaves of the ant-plant *Hirtella myrmecophila*. Although leaf extracts induced recruitment in the ant partner the plant-ant was not able to recognize the extract of the gall tissue (IZZO et al. 2006). The authors argue that the chemical manipulation of the tissue by gall-forming insects should benefit the adult fly at the emergence stage, since tissue rupture remains undetected by the ants. In this stage, cecidomyiid flies are vulnerable to predators because adult emergence and further wing hardening are relatively slow processes.

The change in forest structure and composition indirectly caused by anthropogenic disturbances poses a threat to pioneer trees such as *Neonauclea*. Compared to primary forest, logged-over forest is characterised, among others, by a low tree density and small tree size, both affecting the nesting behaviour of orangutans (ANCRENAZ, CALAQUE & LACKMAN-ANCRENAZ 2004). In the degraded and fragmented forests of Lower Kinabatangan, Sabah, taller *Neonauclea* trees were repeatedly used by the apes as nesting site, causing considerable damage to the plants. Indirect negative effects on plants through human activities have also been documented for a lowland forest in Malaya. In the Pasoh Forest Reserve, pig density has increased 10–100 times beyond historical levels, due to the absence of large predators and an

abundant year-round food supply in the agricultural areas that surround the forest reserve (ICKES, DEWALT & APPANAH 2001). Here, wild pigs snap off stems for nest construction and the surprisingly high impact on the survival of woody saplings is dependent on the ability for resprouting (ICKES, DEWALT & THOMAS 2003).

Ant-plants are also rich and predictable sources of ant prey for predators (GASTREICH 1999, ITINO & ITIOKA 2001, DEBOUT 2004). The damage caused to hosts by myrmecophagous animals has been recorded for many myrmecophytes worldwide (listed in FEDERLE et al. 1999). The domatia of ant-inhabited plants are frequently torn open by predators, mostly birds (woodpeckers), rodents and monkeys. These animals have good cognititve capacities and/or strong mouth-parts and thus appear to be well equipped to locate ant-plants and break open their stem walls. None of these predators, however, has been reported to be a specialist plant-ant predator although plant-ants may provide a staple food source for monkeys (DAVIDSON et al. 2006, ISBELL & YOUNG 2007). Predatory behaviour may often be learned; in some areas, for example, 100 % of all *Macaranga* ant-trees showed unmistakable traces of recent squirrel attacks. As a result, twigs often broke off and some young plants were even killed entirely (FEDERLE et al. 1999). However, the frequency of stem damage varied strongly with different localities, a pattern that is also found among *Cladomyrma* host plants. In a monospecific stand of *Neonauclea gigantea* at a highly disturbed site, 50.4% of all trees (n=226) possessed at least one domatium torn open by predators, assumedly squirrels. In comparison, *Neonauclea* plants growing in forest habitats are much less affected by destructive myrmecophagy. Stem damage caused by predators has also been occasionally observed in other *Cladomyrma* hosts, i.e., *Spatholobus bracteolatus*, *Drypetes longifolia*, *Neonauclea* sp. C, *N. paracyrtopoda*, *Luvunga* sp. and *Crypteronia griffithii*, and thus appears to represent an important cost of myrmecophytism.

The selective advantage provided by domatia to their host plant by mediating mutualistic arthropod presence has been shown both in plant/mite systems (AGRAWAL & KARBAN 1997, ROMERO & BENSON 2004) and in ant/plant systems (FIALA & MASCHWITZ 1992, GAUME et al. 2005). Despite the benefits conferred by myrmecodomatia, however, there may be structural costs associated with them. BROUAT & MCKEY (2001) studied leaf-stem size relationships over ontogeny in three different lineages of hollow-stemmed myrmecophytes and found it to be allometric, in contrast to the isometry previously found in solid-stemmed relatives (BROUAT et al. 1998). The authors hypothesise that the production of domatia is particularly costly for plants early in development due to the requirements of mechanical stability. Hollow stems are generally more likely to break than solid ones (SPATZ, SPECK &

VOGELLEHNER 1990, MATTHECK, BETHGE & WEST 1994), due to local buckling caused by environmental stresses such as wind, rather than the supported weight alone. That caulinary domatia can actually weaken stem stability is suggested by a study of the myrmecophytic tree *Zanthoxylum myriacanthum* (MOOG, FELDHAAR & MASCHWITZ 2002).

Two factors may entail additional costs in terms of stem allocation for ant-plants with caulinary domatia. First, juvenile hosts may require relatively thicker stems, with a thicker ring of tissue around the domatia, to protect initial mutualistic ant colonies from predation (see above). For example, predation may have been a selective force in the evolution of strong thorn domatia of ant-acacias in Central America (JANZEN 1969b). Second, there is a minimum diameter (varying with the ant species) below which a cavity cannot be inhabited (MOOG, DRUDE & MASCHWITZ 1998; this work). Presence of a relatively large cavity or thick pith, easily excavated by mutualistic ants to create a cavity, is thus a prerequisite for the establishment of a mutualistic relationship. Founding queens often colonise stem cavities of very young individuals of myrmecophytes, thereby enhancing both the probability of establishment and ant protection. Selective pressures acting on domatia could have favoured cavities for protective ants that were of habitable size at seedling stages (BROUAT & MCKEY 2000). But expression of domatia in early stages of development certainly increases the allocation of stem tissue in myrmecophytes. Within the *Cladomyrma*/plant system early onset of caulinary domatia is recognised in lianas, which usually have a very small primary diameter (*Callerya*, *Spatholobus*, *Luvunga*), and in the trees *Drypetes* and *Neonauclea*.

11.3. Do host plants need *Cladomyrma* for their survival?

Many studies show that myrmecophytes receive better protection from herbivory (or pathogens and plant competition) when their resident ants are present, and a smaller number even document higher survival rates or higher seed set (reviewed in HEIL & MCKEY 2003). However, the protective functions of the plant-ants may be less obvious, acting in concert to provide a cumulative response becoming visible in long-term studies only (e.g., LETOURNEAU 1998). Nevertheless, several studies demonstrate that myrmecophytic plants are able to survive in the absence of defensive ants (ANDRADE & CARAUTA 1982, FONSECA & GANADE 1996, FÁVERI & VASCONCELOS 2004). In fact, a small but variable proportion of probably *any* myrmecophyte population is not colonised by its (most effective) ant partner (LONGINO 1989, MOOG et al. 2003, SOLANO et al. 2003, FREDERICKSON 2005), and these individuals are not necessarily doomed before reaching the reproductive stage (DEJEAN et al. 2004, 2006). Unfortunately, quantitative data on such observations are often not published.

In the *Cladomyrma*/plant mutualisms hard evidence for lifetime fitness benefits is still missing and quantifying such benefits will be even more difficult for the long-lived host plants of *Cladomyrma*. However, the rate of occupancy by the ant mutualist may give first hints on how host plants depend on the ant partner for their survival.

From table 11-1 it is immediately apparent that *Cladomyrma* hosts differ strongly in terms of occupancy rate. As a rule, data obtained from natural habitats in the field are supported by the herbarium data, with few exceptions. The latter are mostly explained by the sampling method of herbarium material (see table superscripts). The rate of ant occupancy for many species, however, is as high as recorded for other obligate ant/plant mutualisms (e.g., VASCONCELOS 1991, GAUME & MCKEY 1999, FIALA et al. 1999, RAINE et al. 2004). Not surprisingly, hosts of *Cladomyrma* –at least the saplings– having obvious adaptions to house ants, i.e., swollen stems, are characterised by high occupancy rates (*Callerya*, *Drypetes*, *Luvunga*, *Spatholobus*). Similar high occupancy rates are present in hosts with swollen nodes (*Crypteronia*, *Ryparosa*) where the cause of the nodal increase in diameter is less clear and may also be attributable to the mechanical and vascular support of the large leaves.

In *Neonauclea* ant-plants, providing the most conspicuous domatia with prostomata for their ant partner, the average occupancy rate (70%) is somewhat lower than expected (Tab. 11-1). By comparing the rates of occupancy for different habitats it is suggested, first, that the high ecological amplitudes of the *Neonauclea* species, growing in the forest understorey, along river banks, land slides, tree fall gaps and even in large man-made disturbances (*N. gigantea*), exceeds those of its *Cladomyrma* partners or, second, that *Neonauclea* can establish in areas away from *Cladomyrma* sources.

The first cause, the ability of *Neonauclea* to colonise a wider range of habitats than *Cladomyrma*, is only in part supported by the available data. The ants have been found in all habitats, from the shaded forest understorey to areas characterised by fragments of logged over forest, plantations and fallow land. Altitude, however, appears to be a limiting ecological factor. A few individuals of *Neonauclea gigantea* and *N. pseudocalycina* were found up to 1,650 and 1,500 m, respectively, well above the elevational limit of *Cladomyrma* (*c*. 1,350 m). Occupancy rate also appeared to be affected by disturbance regime. The few observations presently available point to lower occupancy rates of *Neonauclea* at sites where myrmecophagous predators had left unmistakable marks on domatia. These sites were commonly found in areas of anthropogenic disturbances where *Neonauclea* may form monospecific stands, rather than in those of small natural disturbances in forests.

Table 11-1: Occupancy rates of host plants by *Cladomyrma* (generalist ants as secondary colonisers are not included). Occupancy rate [%] is given for plants examined in the field and for herbarium material (sample size *n* is given in parentheses). Data obtained from herbar specimens are conservative estimates because specimens with ambiguous signs of *Cladomyrma* colonisation are excluded. Occupancy rates are also provided for selected groups of the populations studied, i.e., size ranges where the smallest (or tallest) plants are omitted, different habitats or high altitudes. MP = Malay Peninsula, B = Borneo.

plant taxon	range of tree height or liana length [m]	occupancy rate [%] (*n*)		occupancy rate [%] (*n*)	
		field	herbarium	by size range, habitat or altitude (field data only)	
Callerya nieuwenhuisii	1.1–35	**100** (35)	**82** (26)		
Crypteronia griffithii	0.3–30	**86** (203)	**9** [1] (90)	0.5–30 m:	**93** (187)
				1–15 m:	**100** (149)
				15–30 m:	**0** (6)
C. macrophylla	5–20		**90** (20)		
Drypetes fusiformis	5–35		**40** (5)		
D. longifolia (MP)	0.73–14	**93** (15)	**14** [2] (35)	1.1–14 m:	**100** (14)
D. longifolia (B)	0.28–12	**95** (101)	**70** (70)	0.5–12 m:	**100** (96)
Luvunga sp.	0.4–8	**86** (35)	– [3]	0.8–8 m:	**100** (20)
Neonauclea spp. (eight species pooled)	0.2–25	**70** (579)	**45** [4] (157)	forest:	**86** (42)
				forest fringes:	**78** (37)
				disturbed:	**72** (81)
				strongly disturbed:	**56** (419)
				> 1350 m alt.:	**0** (11)
Ryparosa anterides	20–40		**72** (18)		
R. fasciculata	0.35–16	**91** (47)	**80** (15)	1.4–16 m:	**100** (34)
R. porcata	?–18		**100** (3)		
R. sp. nov. aff. *calotricha*	?–30		**75** (4)		
Saraca dives	5–20	**45** [5] (15)	**67** (3)		
S. thaipingensis	0.6–25	**53** (280)	**42** (86)	forest [6]:	**86** (142)
Spatholobus bracteolatus	1.1–33	**98** (52)	**100** (1)	1.2–33 m:	**100** (51)
S. oblongifolius	0.4–28	**100** (44)	**68** [7] (41)		
Strychnos vanprukii	0.7–12	**35** (101)	**17** [8] (6)		

Superscript: [1] Herbarium data do not correspond to the field data because herbar specimens were collected from mature flowering trees who lose their ant mutualist; [2] The low proportion of occupied herbarium specimens is attributable to the sampling of distal, non-swollen stem parts by the collectors, rather than a dissolution of the association. About 2/3 of the herbar specimens classified as 'not colonised' had twig diameters too small for ant-housing. Several herbarium specimens exhibited ambiguous signs of ant colonisation. If they are included occupancy rate reaches 31%; [3] Species determination in the genus is a great mess. Herbar specimens assigned to at least three species showed signs of *Cladomyrma* colonisation and apparently belong to a single species; [4] The low percentage obtained from herbarium material is an artefact and reflects the sampling of flowering branch tips by botanists, thus often missing the adjacent domatium; [5] Occupancy rate is probably underestimated because branches of 11 trees were out of reach (>3 m; see EGUCHI & BUI 2007); [6] The 'forest' habitat excludes a strip along the river banks at the study site where the average size of the *Saraca* trees is distinctly increased; [7] Twelve percent of the herbarium specimens exhibited ambiguous signs of ant colonisation. If they are included occupancy rate reaches 80%; [8] Due to inadequate taxonomy only herbar specimens from the Malay Peninsula are taken into account. The low percentage reflects the fact that *Cladomyrma* inhabitation of *Strychnos* is often restricted to a small portion of the plant, and it may thus be missed by a collector.

Distance between populations affects the rate of occupancy probably to a greater extent as habitat type. All members of *Neonauclea* produce small wind-dispersed seeds allowing *Neonauclea* species to reach new suitable habitats outside the range of founding *Cladomyrma* queens resident in the parent population. Following roads leading away from forests rich of *Cladomyrma*/*Neonauclea* associations I observed a continuous decrease or a sharp break in the rate of occupancy when distances between stands of *Neonauclea* increased and/or when a vegetation cover connecting these stands was lacking.

To summarise, unoccupied *Neonauclea* –whether the reason is altitude, distance to *Cladomyrma* sources or disturbance (myrmecophagy)– all bore domatia and on some of these plants the remains of older inflorescences were seen. It is thus indicated that the presence of *Cladomyrma* is, at the individual level, not an indispensable prerequisite for *Neonauclea* to reach the reproductive stage. However, the absence of myrmecophytic *Neonauclea* species outside the range of their ant partners on a geographical scale (RAZAFIMANDIMBISON et al. 2005) seems to support the conclusions of BLATTNER et al. (2001) that the establishment of new myrmecophytic populations in new habitats is dependent upon the availability of their specific ant partners. This would also imply that obligate mutualistic ant–plant associations, to some extent, limit vagility of myrmecophytes.

The discrepancy in occupancy rate between field and herbarium data in *Crypteronia griffithii* (Tab. 11-1) is not the result of sampling method or habitat type but appears to reflect a dissolution of the mutualistic interaction. The very low proportion of colonised adult flowering trees derived from herbarium material (see Fig. 4-42, 4-43) is consistent with the observation that all six adult *C. griffithii* checked in the field (15–30 m in height) were not occupied by their ant associate. Because *Cladomyrma maschwitzi* is the smallest species in the genus and colonises stems of a relatively thin diameter (Fig. 4-41) the lack of ant colonisation in most herbarium specimens, which are all collected from flowering trees, is thus likely not an artefact.

It is assumed that death of a queen of *Cladomyrma maschwitzi*, and subsequently of the queen-less colony, usually occurs prior to the reproductive onset of *Crypteronia griffithii*. Although astounding figures for the lifespan in ant queens, e.g., ranging for several species of other formicine genera like *Camponotus*, *Formica*, and *Lasius*, from max. 20 to 28.5 years (under laboratory conditions), have been recorded (KELLER 1998), *C. maschwitzi* queens may not reach the age necessary to keep up with the lifespan of the host tree. Exact growth rates of *Crypteronia griffithii* are not known but it is estimated that the tree may reach reproductive onset earliest after 10–15 years

(MOOG, DRUDE & MASCHWITZ 1998), thus leading to a disassociation of the ant-plant mutualism in reproductive trees. A limitation to this assumption is the fact that I do not know whether orphaned mature *Cladomyrma* colonies may be able to adopt new queens. However, adoption of new queens in monogynous ant species has been rarely documented (GADAU et al. 1998, FELDHAAR et al. 2000). The second host species in the genus *Crypteronia*, *C. macrophylla*, differs from *C. griffithii* by maintaining the mutualism during the reproductive stage, probably because the species flowers earlier in ontogeny –within the lifespan of *Cladomyrma*– than *C. griffithii*, as it is indicated by a significantly smaller tree height of flowering specimens (Fig. 4-48).

A change in the life history of a *Cladomyrma*/plant mutualism also occurs in the host tree *Saraca thaipingensis*. Larger and hence older trees have a distinctly lower rate of occupancy by *Cladomyrma* ants (Fig. 4-3). In addition, the overall occupancy rate is markedly lower than in most other host species of *Cladomyrma* (Tab. 11-1). In this system, *Cladomyrma* not only competes with a generalist stem-dwelling *Crematogaster* species (Fig. 4-5) but is also mostly confined to plants of smaller size classes in the forest understorey. In fact, *Saraca thaipingensis* can be found outside forested areas in rural land and is even planted as an ornamental tree near shrines and in parks because of its lovely blooms. Here, trees lack stem-dwelling ants and they appear to be independent of the ants' antiherbivore protection.

In terms of occupancy rate and pattern of inhabitation the woody climber *Strychnos vanprukii* stands out among *Cladomyrma* hosts. First, although *Strychnos vanprukii* is described as a wide-ranging species (south and northeast India, Laos, Vietnam, Thailand, Malay Peninsula and Borneo) inhabitation by *Cladomyrma* has only been established for two localities in the Malay Peninsula. [But because the Malayan material differs in several characters from specimens of Continental Asia and Borneo species delimitation of this taxon should be redressed.] Second, occupancy rate at the study sites was surprisingly low (35%). Moreover, about half of the occupied plants harboured a single colony founding queen without workers. If only colonies are considered, occupancy rate is even lower (16%). Third, ant colony size was usually small without alate sexuals and, correspondingly, only a small proportion of a plant's available internodes were inhabited (see page 76).

These features of the *Strychnos*/*Cladomyrma* association contrast sharply with the remaining *Cladomyrma* systems. Coupled with the obvious lack of stem modifications facilitating ant mutualism the association may represent an initial stage of a host

expansion process by *Cladomyrma* (see page 151 and 327). This would explain why *Strychnos vanprukii* appears to have a 'weak' relationship with *Cladomyrma*.

To sum up, several factors have been identified which may account for unoccupied hosts of *Cladomyrma*. First, plants which were once mutualistic no longer interact with the ants and the mutualism may disassociate with ontogeny (*Crypteronia griffithii*, *Saraca thaipingensis*). Second, disturbances such as myrmecophagy may locally produce ant-free trees. Third, the distance to *Cladomyrma* sources is, in some areas, thought to explain unoccupied trees in wind-dispersed *Neonauclea*. Fourth, hosts may dwell in habitats unsuitable for *Cladomyrma* (*Neonauclea* at high elevations). And last, the association may be of recent origin and thus in an evolutionary initial stage (*Strychnos*) or, alternatively, selective pressures act on the association in different directions and thus hinder its further specialisation.

At a geographical scale, three species have been recorded from areas outside the range of their ant partners (*Saraca thaipingensis*, *Drypetes longifolia* and *Strychnos vanprukii*). However, except for *Saraca*, the species boundaries of these taxa are apparently too broadly defined and, in my opinion, need a thorough revision. The differences among the herbarium material collected from different geographical areas justify, at least, the recognition of segregate subspecific taxa. Specimens of *Saraca thaipingensis* from west and central Java (n=9) bore no signs of ant inhabitation, and *S. thaipingensis* apparently thrive in these areas in the absence of *Cladomyrma*.

Examples for the loss of the ant mutualist have also been documented in other ant/plant systems. Myrmecophytic *Cecropia obtusifolia* on Hawaii, introduced through human activity, lack ant association in the stems and the Müllerian (food) bodies are left unharvested. Moreover, no evidence was found that generalist ants visiting the plant's surface or tending hemipterans were providing benefits to the *Cecropia* trees (WETTERER 1997). Thus the success of *C. obtusifolia* on Hawaii suggests that this species is not obligately dependent on mutualist *Azteca* ants. However, most Neotropical herbivores and competitors may be absent in Hawaii.

A case where the distance to native forests, i.e., ant sources, negatively affects the rate of ant occupancy has been reported from urban San José in Costa Rica (WETTERER 1998). Occupancy rate of Costa Rican *Cecropia obtusifolia* by *Azteca* ants was much lower (7%) than in natural habitats (86%; LONGINO 1989). Further evidence demonstrates that an ant/plant mutualism can evolutionarily disintegrate without the loss of both partners if the proper habitats are available. For example, *Cecropia 'peltata'* is not occupied by ants on Puerto Rico and most other Caribbean islands and,

on the mainland, some high-elevation *Cecropia* have also lost the mutualistic interaction with *Azteca* (JANZEN 1973). Even the progressive loss of ant-related traits is known from *C. 'peltata'* occurring outside its natural distribution (JANZEN 1973, RICKSON 1977, MCKEY 1988b, PUTZ & HOLBROOK 1988).

11.4. The ants' point of view

The benefits for *Cladomyrma* ants colonising myrmecophytic plants are quite evident – domicile and food in one convenient place. By excavating live stems of their hosts the ants gain a long-lived, well-protected, weather-proof nest site as well as a secure feeding substrate for the associated trophobiotic coccoids. Access points to the nest are restricted to small orifices which can be easily defended against a wide range of competitors, parasitoids and predatory arthropods. Host plants that provide stems of sufficient dimensions for foundress queens in the seedling or sapling stage allow an early establishment on, and monopolisation of, the host, interspecific competition is thereby likely reduced. Furthermore, ant activities on the plant surface such as foraging or patrolling are always close to nest entrances and in the face of danger escape routes for ant workers are short.

Since the ant's mode of life is tightly linked to that of the host plant, the ants share with their host some handicaps of the sedentary lifestyle. They cannot move to another site when conditions become unfavourable. Predators of ants such as birds, monkeys or some rodents (see above) may learn to recognise host plants as regular food sources. Furthermore, plant-ants such as *Cladomyrma* face the problem to meet their nutritional demands solely from plant-derived food sources, only supplemented by occasional prey hunt down on the plant surface. The plants often represent almost the entire universe of resources required by the ants. Plant-derived rewards, directly via extrafloral nectar or food bodies or indirectly via exudates of trophobiotic hemipterans, are energy-rich but usually nitrogen-poor (DAVIDSON et al. 2003). Two *Cladomyrma* species studied had strikingly low $\delta^{15}N$ ratios typical for many plant-ants; this indicates nitrogen sources other than predation or scavenging (DAVIDSON et al. 2003). [With each trophic level the heavier isotope ^{15}N is enriched relative to ^{14}N. In general, ^{15}N increases by 3–4‰ with each increasing trophic level.]

There are many reports in the literature describing symbiotic relationships between microorganisms and insects (e.g., DOUGLAS 1998, BOURSAUX-EUDE & GROSS 2000). Indeed, it was estimated that at least 15–20% of all insects live in symbiotic relationships with microorganisms (BUCHNER 1965). For example, endosymbionts supplement the nutrient poor diet of Hemiptera that feed on plant sap by synthesizing critical amino acids (DAVIDSON & PATRELL-KIM 1996) and such tight, vertically

transmitted associations can lead to congruent phylogenies of the interacting taxa (DOWNIE & GULLAN 2005). In the past few years new insights into the symbiosis of ants and microorganisms have been reported. Examples are the symbioses of the ant genera *Camponotus* and *Tetraponera* with intracellular bacteria (SCHRÖDER et al. 1996, VAN BORM et al. 2002, FELDHAAR et al. 2007). Plant-ants may also have evolved several strategies to compensate for nutritional imbalance (MCKEY et al. 2005), including bacterial endosymbioses. Abundant endosymbionts found in the hindguts of the African plant-ant genera *Aphomomyrmex* and *Petalomyrmex* may suggest a function in nutritional upgrading (MCKEY et al. 2005). Stoichiometric analysis of the *Cladomyrma*-coccoid-plant system and studies of (potential) gut symbionts are now necessary to explore its trophic structure.

In ant/plant mutualisms the partners disperse independently of each other (horizontal transmission) and are formed anew each generation. Most of the ant mutualists are forest-dwelling species and, therefore, founding queens must be able to locate their host plants against a diverse background of plants. In the Pasoh 50-hectare plot, a lowland dipterocarp forest in Malaysia, specificity of colonisation of myrmecophytic *Macaranga* plants was also maintained at rather isolated sites, such as forest gaps, despite rather distant and hidden occurrence of individuals (MOOG et al. 2003). In the *Cladomyrma* system spatial heterogeneity of host plant densities is pronounced. Whereas some hosts may be locally abundant (*Neonauclea*, *Saraca*), others are usually rare (*Drypetes*, *Luvunga*, *Ryparosa*) or confined to rather narrow habitats (Malayan *Spatholobus*: hill forest between 800 to 1,350 m a.s.l.). Host plant densities have been measured at some localities and, in a few cases, they were as low as 0.5–2 ha^{-1}.

New foundress queens of *Cladomyrma* leave their natal host, mate, and then attempt to locate uncolonised host plants. To the ants the potential hosts are scattered in the forest as islands in an ocean. Attraction from a distance may involve olfaction, vision, or both. It has been shown for other ant/plant systems that volatile compounds of host plants play a crucial role as olfactory cues in host localisation (*Cordia*: EDWARDS et al. 2006; *Macaranga*: JÜRGENS et al. 2006). *Cladomyrma* foundress queens have been found in areas with low host plant density, at distance from source ant colonies and in hidden locations, which suggests that foundresses use olfactory cues in long-range detection of host plants. Search capabilities of *Cladomyrma* queens thus appear to be well developed. Preliminary results on host-choice by *C. petalae* queens are presented in chapter 5, p. 166.

11.5. Host specificity

In ant/plant mutualisms, ant colonies live on hosts for the entire colony cycle, and the associations are obligate for one or both partners. Such close relationships are thought to favour species-specificity and diversification (JANZEN 1980, SCHEMSKE 1983, THOMPSON 2002). Although obligate plant-ants show considerable conservatism of host plant use worldwide, few have been reported to utilise a single host species (MCKEY 1984, WARD 1991, CLARKE & KITCHING 1995, LONGINO 2006). Strict pairwise associations may occur for a given species at a local scale (FIALA et al. 1999) but more partners are utilised in other parts of its geographical range. In most cases, however, plant-ants and/or their myrmecophytic hosts are associated with a (small) set of partner species (see review by DAVIDSON & MCKEY 1993a). Several ant/plant systems also include live-stem inhabiting ant species that are not restricted to one or a few host species, but instead are found in a variety of different, unrelated ant-plants (e.g., *Allomerus*: FONSECA & GANADE 1996; *Azteca*: LONGINO 1996; *Myrmelachista*: LONGINO 2006; *Pseudomyrmex*: WARD 1999). This phenomenon –specificity of host plant usage in most species, but promiscuous associations by some– is also a characteristic pattern in the *Cladomyrma* system.

As currently known, the 12+ species of *Cladomyrma* obligately colonise 24 plant species belonging to a surprisingly extensive range of plant taxa (Tab. 4-6): *Callerya*, *Saraca*, *Spatholobus* (Fabaceae), *Crypteronia* (Crypteroniaceae), *Drypetes* (Putranjivaceae), *Ryparosa* (Achariaceae), *Strychnos* (Loganiaceae), *Neonauclea* (Rubiaceae), *Luvunga* (Rutaceae) and *Sphenodesme* (Lamiaceae). These 10 host plant genera from eight plant families comprise about 50% of all non-epiphytic plant genera, which are known to be regularly associated with specialised stem-nesting ant partners in the Oriental region (MOOG et al. 2003). In terms of taxonomic diversity on the genus and family level the range of hosts utilised by *Cladomyrma* is one of the broadest ever recorded for any live stem-nesting plant-ant lineage worldwide (Fig. 11-1).

Most *Cladomyrma* species have been recorded from only one or two (three) host plant species (*andrei*, *crypteroniae*, *hobbyi*, *maschwitzi*, *nudidorsalis*, *scopulosa*, *yongi*), but two species show a different pattern of host affiliation. *Cladomyrma petalae* and *C. dianeae* are more catholic in their host usage, the first being a ‘generalist’ plant-ant colonising hosts across a broad taxonomic range, the second inhabiting several members of the genus *Neonauclea* (Fig. 11-1).

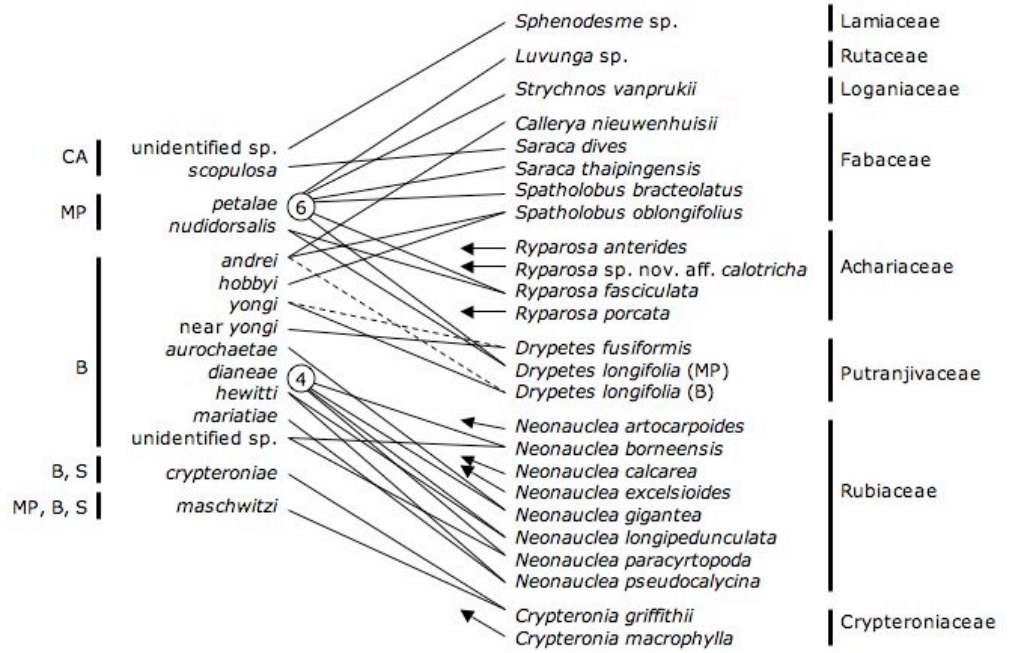


Figure 11-1: Host specificity and promiscuity of *Cladomyrma* species, showing geographic regions (CA = Continental Asia [Thailand, Vietnam], MP = Malay Peninsula, B = Borneo, S = Sumatra) and plant taxa. Black lines join *Cladomyrma* species to their hosts; dotted lines indicate pairings with uncertain ant identification; arrows stand for colonisations by *Cladomyrma* as derived from the examination of herbarium specimens (*Cladomyrma* species not known). Some of the observed associations in the *Neonauclea* complex are not included (*Neonauclea* sp. A – E; see page 135–139) because these informal taxa are probably represented by several of the species listed. For two *Cladomyrma* species the number of known host plant species is indicated: *C. petalae* colonises six unrelated hosts, whereas *C. dianeae* inhabits at least four hosts, all belonging to the genus *Neonauclea*. The other *Cladomyrma* species appear to have a restricted host range, with one or two partner plants.

However, a note of caution should be addressed regarding host affiliations of *Cladomyrma*. The picture presented to date is far from complete: a) my survey could not cover all regions and habitats; b) sampling size differed greatly between host species due to the low density or rarity of some taxa; c) some host records, e.g., three *Ryparosa* spp. and *Crypteronia macrophylla*, are based solely on herbarium specimens; d) the relative proportion of host usage is often not known, increased sampling might show that a particular host record is rather an exception or mismatch; e) taxonomic uncertainties may cause a diffuse pattern of species pairings, especially within myrmecophytic *Neoauclea*. Young sterile plants of this genus could often not be identified to species level because a key for vegetative characters has not been developed (RIDSDALE 1989). Moreover, hybridisation among myrmecophytic *Neonauclea* appears to occur (RAZAFIMANDIMBISON et al. 2005) and this will add another level of complexity.

Despite these limitations, the gross pattern emerging from the data currently available is probably quite robust. One *Cladomyrma* species shows an extremely 'promiscuous' host usage, increased sampling will only expand the already known broad host range. A set of species is restricted to *Neonauclea*, the only host genus with a considerable radiation of myrmecophytic species in the system, and at least one ant species appears to colonise several *Neonauclea* species. Species associated with *Neonauclea* have not been found on other sympatric host plants (*Callerya*, *Drypetes*, *Spatholobus*). The species *Cladomyrma maschwitzi* is almost certainly restricted to one or two species of *Crypteronia*. Even in extensively studied areas with quite a number of sympatric *Cladomyrma* host plant species (Ulu Gombak, Selangor, and Lambir Hills, Sarawak), *C. maschwitzi* has never been recorded away from *Crypteronia*. Vice versa, the host *Crypteronia griffithii* was never found to harbour *Cladomyrma* species other than *C. maschwitzi* or *C. crypteroniae*. The apparent similar narrow host ranges of *Cladomyrma* species inhabiting Bornean *Callerya*, *Drypetes* and *Spatholobus* need to be verified, but the general pattern of *Cladomyrma* host affiliation is represented by two poles: a species-specific and a promiscuous usage of host plants.

What causes prevent ants from colonising plants other than their 'usual' hosts? Determinants of species-specificity have been intensely studied in many organisms, and here I present a non-exhaustive list of (not mutually exclusive) factors promoting host-specificity:

Phylogenetic constraints: parasitoid tachinid flies: STIREMAN & SINGER 2003; leaf beetles: FUTUYMA 2000; papilionoid butterflies: FIEDLER 1998; Lycaenidae: FIEDLER 1997; thrips: CRESPI et al. 1998.

Poor-quality hosts (post-colonisation process): inadequate internode size or food supply might limit colony establishment of plant-ants: DAVIDSON & FISHER 1991, YU & DAVIDSON 1997, NERY & VASCONCELOS 2003.

Niche partitioning: mycorrhizal fungi: BEVER et al. 2001; physical barriers act as ecological filters in ant-plants: trichomes (DAVIDSON, SNELLING & LONGINO 1989) and waxy stems (FEDERLE et al. 1997).

Interspecific competition: plant-ants: FEDERLE, MASCHWITZ & HÖLLDOBLER 2002, PALMER, STANTON & YOUNG 2003, SOLANO et al. 2003, DJIETO-LORDON et al. 2004.

Habitat specificity: weevils: JONES 2001; plant-ants: DAVIDSON et al. 1991, YU & DAVIDSON 1997. Host and habitat specificity are often confounded due to habitat specialisation by hosts. In such cases, ecological species sorting cannot be separated from evolved host specificity.

Host location efficacy: fig wasps, GRISON-PIGÉ et al. 2002; plant-ants: MURASE et al. 2002, JÜRGENS et al. 2006, GRANGIER et al. 2009.

Host discrimination capability: specialists are better in distinguishing 'good' hosts from 'poor' hosts; aphids: BERNAYS & FUNK 1999; due to limitations in the ability to perceive and integrate host-associated stimuli insects may drop suitable hosts when such plants are difficult to discriminate from unsuitable hosts: FOX & LALONDE 1993.

Several of these mechanisms are potential determinants of host specificity in the *Cladomyrma* system. It is unlikely, however, that a single mechanism is responsible for the observed pattern of species pairings. Selection may have fine-tuned ant physiology and host-finding to be more efficient on a particular host. Differences between hosts in stem structure, suitability as substrate for trophobiotic scale insects, growth and habitat may all influence queen mortality, colony growth or brood production.

For example, some neotropical *Cecropia* are dominated by *Azteca australis*, which tends to prefer hosts with especially high production of pearl bodies. Also, *Pachycondyla luteola*, a regular occupant of *Cecropia pungara*, fails to produce larvae and pupae on *C. membranacea* probably due to the inadequate pearl bodies of the latter (YU & DAVIDSON 1997). It is suggested that *P. luteola* queens only colonise the 'poor' host after saplings of the 'good' host became saturated with colonising queens. Two other ant species associated with *Cecropia* trees, *Azetca ovaticeps* and *Camponotus balzani*, appear to be habitat specialists but host generalists (YU & DAVIDSON 1997). Host-choice in the former might be explicable by queen orientation to natal hosts, and that of the latter species is probably dependent on a suitable internode size of *Cecropia* saplings. Multiple mechanisms for host-specificity may be characteristic of relationships in which partner species show horizontal transmission, i.e., disperse separately from one another. This is an agreement with the view that cocladogenesis, the pairwise reciprocal speciation leading to topological identical phylogenies of host and associate, is more likely in systems where dispersal of mutualists is tightly coupled (THOMPSON 2002).

11.6. Host range and specialisation in other plant-ant lineages

The degree and pattern of specialisation among species is one of the most central problems in the evolution of species interactions. The proportion of specialists and relative generalists in species interactions differs among lineages.

This is exemplified by the best-known Asian ant-plant mutualism. Recent studies on the *Macaranga*/*Crematogaster* system revealed an absence of overall phylogenetic congruence between ants and plants (FELDHAAR et al. 2003, QUEK et al. 2004). In most cases, *Crematogaster* (*Decacrema*) ants are specific to host clades, rather than to individual host species. Some ant taxa even occur on hosts belonging to different clades. These results support the view that host shifting or host expansion is common in the ants colonising *Macaranga* (FIALA et al. 1999, FELDHAAR et al. 2003). Despite the absence of cospeciation, host shifts or host expansions of *Decacrema* have been constrained by stem traits (waxy or non-waxy) that are themselves constrained by *Macaranga* phylogeny (QUEK et al. 2004, FEDERLE & RHEINDT 2005). This suggests that ants and plants have diversified in association, or codiversified.

Studies on other ant/plant mutualisms are in accordance with the hypothesis that codiversification and host shifts or host expansions, rather than cospeciation, shape the pattern of species interactions in these systems (*Azteca*/*Cecropia*: AYALA et al. 1996; *Azteca*/non-*Cecropia*: LONGINO 1996). A similarly diffuse pattern of coevolution was inferred for the acacia-ants of the *Pseudomyrmex ferrugineus* group (JANZEN 1966, WARD 1993). This is also consistent with the taxonomically diverse array of myrmecophytes that are utilised by ants in several systems. For example, the host range of the pseudomyrmecine plant-ants *Pseudomyrmex*, *Tetraponera* and *Myrcidris* encompass 12 plant families and 19 genera (WARD & DOWNIE 2005). The principal ant-plants are *Tachigali* (Fabaceae) and *Triplaris* (Polygonaceae). Molecular data strongly support that *Triplaris* ants and the *Tachigali* ants have independently evolved from different groups of generalist *Pseudomyrmex* that inhabit dead twigs (WARD & DOWNIE 2005). However, the ants living in *Triplaris* and *Tachigali* have convergently evolved similar traits, such as shorter antennal scapes, reduced eyes, and more robust petioles. Earlier phylogenies, based on morphological data alone, placed them in the same species group and were thus misleading (WARD 1991). Pseudomyrmecines appear to be particularly prone to establishing close (and often mutualistic) relationships with plants. Mapping ant–plant associations on the phylogeny of Pseudomyrmecinae leads to the conclusion that such associations arose at least twelve times (WARD & DOWNIE 2005). In general, the diversity of many of these ant/plant associations appears to result both from the convergence of unrelated taxa and diversification within taxa.

In comparison with *Cladomyrma*, the associations of the neotropical, exclusively arboreal ant genus *Myrmelachista* with plants is perhaps the most similar ant/plant system with regard to ecology and pattern of host affiliation. It is a community of small, coccoid-tending ants, nesting in a taxonomically diverse array of plants (SCHUMANN

1888, ULE 1906, SKWARRA 1935, STOUT 1979, NESOM & STUESSY 1982, BENSON 1985, KETTERL et al. 2003, MEHLTRETER, ROJAS & PALACIOS-RIOS 2003, LONGINO 2006, GOITÍA & JAFFÉ 2009). In total, host plants have been recorded from at least 25 plant genera and 17 families. If generalist species which nest in dead wood or preformed chambers produced by stem-boring insects are excluded, the number of hosts is still impressive, comprising about 19 plant genera from 12 families. Some *Myrmelachista* maintain two-species or monospecific 'devil-gardens' of their host plants (*Duroia hirsuta*, *Cordia nodosa*, *Tococa occidentalis*) by poisoning all plants except their myrmecophytic hosts with formic acid (DAVIDSON & MCKEY 1993b, FREDERICKSON, GREEN & GORDON 2005).

Despite the number of scattered host records, *Myrmelachista* species are inconspicuous and have been little studied. Many of these species nest cryptically inside of live stems of understorey Lauraceae and their host plants obviously show no external signs of specialisation for ant occupation. There are no preformed domatia, no food bodies, and no extrafloral nectaries (LONGINO 2006), but JANZEN (1974, p. 257) in his work on Bornean epiphytic myrmecophytes alluded to the *Myrmelachista*/*Ocotea* mutualism: "*At the point of entry the wall is exceptionally thin, and such spots are formed at regular intervals along the stem*." This observation indicates the presence of preformed prostomata that facilitate entry into internodes. In a study on tree architecture of *Ocotea* species, ISHI & ICKES (1995) found no differences between myrmecophytic and non-myrmecophytic species in branch diameter. However, myrmecophytic species had larger leaves and a shorter branch length (relative to diameter). It is unclear if these differences are the result of modifications exerted by the ants on the plants' architecture over evolutionary time or if they are caused by e.g., adaptation of the plants to moist, shady habitats (GIVNISH 1987). One *Myrmelachista* species, *M. ulei*, has been reported to regularly inhabit the swollen twigs of the understorey melastome shrub *Pterocladon sprucei* Hook. f. (ULE 1906; synonym of *Miconia bailloniana* Macbr.). These anecdotal reports suggest that hidden or slight modifications of stem structure in host plants of *Myrmelachista* may be more common than is currently recognised. Within the host plant spectrum of *Myrmelachista*, however, several hosts clearly produce structures adapted for ant housing (e.g., *Clidemia*, *Cordia*, *Duroia*, *Tachigali*, *Tococa*). Note that these domatia may have evolved in response to ant inhabitants other than *Myrmelachista*, because members of several plant-ant genera may colonise these plants.

In short, many *Myrmelachista*/plant associations exhibit several characteristic features which they share with those of *Cladomyrma*:

- cryptic lifestyle in live stems
- tending of scale insects inside stems for honeydew (plants provide no extrafloral nectar or food bodies)
- several host plants do not possess conspicuous adaptions for ant occupation (despite regular inhabitation by ants)
- pruning of vines is deployed in different degrees by the ants (DAVIDSON & MCKEY 1993b)
- 'neophily', ants preferentially patrol young plant tissue (STOUT 1979)
- broad host range, including plants of the shaded understorey
- species vary in host specificity: some are generalist dead-stem nesters; others always use live stems, but not of particular species of plants; still others are variously specialised on particular lineages of plants [In contrast to *Myrmelachista*, dead-stem nesting *Cadomyrma* have never been found.]

Interestingly, as in some *Myrmelachista*, at least one *Cladomyrma* species, *C. maschwitzi*, employs chemical 'warfare' against vines by spraying formic acid into the wounds after biting (MASCHWITZ, DUMPERT & MOOG, in prep.). Recent studies suggest that *Myrmelachista* and *Cladomyrma* are closely related (LAPOLLA et al. 2006, LAPOLLA & LONGINO 2006), and the two genera –possessing a similar combination of traits– appear to have conserved the potential to colonise, over evolutionary time, new hosts possessing no myrmecophytic specialisations.

In the following I propose a scenario in which three key traits of *Cladomyrma* are hypothesised to promote the acquisition of new host plants in the course of evolution. This scenario might also apply to the *Myrmelachista* system, but despite being species-rich and abundant, studies on *Myrmelachista* ecology and natural history are surprisingly rare.

11.7. Evolution of host affiliation

As shown above, a number of both obligate myrmecophytes and plant-ants are known to have multiple associates. In the majority of cases they appear to have arisen by repeated de novo colonisation or host switching and host expansion over evolutionary time, rather than through strict cocladogenesis of two interacting lineages. What traits may function as evolutionary routes to obligate associations of ants and plants?

Access to living stems: A hypothesis put forward by BENSON (1985) and WARD (1991) states that the primary origin of ant-myrmecophyte associations may lie in the tendency of ants to occupy cavities in live plant stems created by wood-boring insects. Once ants, and especially ant queens, acquired the ability to bite into living plant parts, they circumvent reliance on stem-boring insects and greatly increase the number of potential sites for colony-foundation. This trait, in turn, is expected to favour the acquisition of new hosts in different plant taxa. I suggest that 'live plant excavation' by colony-founding queens is an ancestral trait in *Cladomyrma*. This work has shown that all *Cladomyrma* queens maintain the ability to chew through woody stems and hollow out live stems for colony-foundation. As a rule, they are the first colonisers in any host plant studied; priority of access then secures the subsequent monopolisation of the host. In contrast, plant-ants that have adapted to hosts with specialised 'entry points', so-called prostomata, may have lost the ability to colonise unspecialised stems of other plant taxa.

Independence from direct, plant-derived food rewards: The predominant food source of *Cladomyrma* appears to be the honeydew of scale insects which the ants tend inside their nest cavities. [In case trophobionts are also sometimes preyed upon by the ants, which is not known from the *Cladomyrma* system, the coccoids may also assure a regular and predictable supply of protein.] Hence, *Cladomyrma* can thrive in plants that provide no direct, specialised food reward such as food bodies or extrafloral nectar. However, the establishment of such a tripartite symbiosis (plant, ant and scale insect) in newly acquired hosts requires two important conditions. First, the coccoids must arrive at the plant and need to enter colony-founding chambers. Second, scale insects should be extremely polyphagous and/or *Cladomyrma* should be capable to associate with a large variety of generalist or already host-specific trophobionts.

Both requirements hold for the *Cladomyrma* system. Data on scale insect acquisition by *Cladomyrma* foundress queens (chapter 6) show that hemipteran trophobionts are not transported by the queens on their nuptial flight but they nevertheless arrive on the host plant independently of the ants, probably via wind dispersal of crawlers. Entry into nest chambers is facilitated by holes kept open by the foundress queen. Furthermore, the coccoid taxa tended by *Cladomyrma* belong to a large variety of species, probably including 30 or more species. They comprise members of Coccidae and Pseudococcidae from the genera *Coccus*, *Crenicoccus*, *Crisicoccus, Exallo-mochlus*, *Hordeolicoccus*, *Maconellicoccus*, *Paracoccus*, *Paraputo*, *Planococcus*, and *Pseudococcus* (WILLIAMS 2004, MOOG et al. 2005). Some of the collected coccoid species, such as *Maconellicoccus multipori*, *Planococcus lilacinus*, *P. minor*,

Pseudococcus cryptus and *Coccus secretus*, are known to have an extreme broad host plant range, including hundreds of host species from dozens of families (BEN-DOV, MILLER & GIBSON 2009); yet others, such as species of the recently described genus *Crenicoccus*, have been found only in association with *Cladomyrma* ants on a few host species (WILLIAMS 2004).

The prevalence of coccoids in ant-plant mutualisms suggest that they generally play an important role in the evolution of ant/plant symbioses (WARD 1991). Is it indeed the case that coccoids are always an integral component in the origin of ant–plant mutualisms? In the Asian *Crematogaster*/*Macaranga* mutualism, ants tend *Coccus* scale insects, forming a tripartite symbiosis (HECKROTH et al. 1998). However, a recent phylogenetic study of the scale insects collected from myrmecophytic *Macaranga* – estimating their time of origin based on a mitochondrial COI molecular clock– suggests that they were latecomers in the evolutionary history of the symbiosis (UEDA et al. 2008). In contrast to the *Cladomyrma* and many other tropical ant/plant systems (see above), intergeneric host shifts are absent from the *Crematogaster*/*Macaranga* mutualism. In the origin of this unique symbiosis, the ants may have first relied on extrafloral nectaries in place of coccoids or they may have relied only on food bodies provisioned by the plants (UEDA et al. 2008).

Behavioural traits being of potential benefit to the host: All *Cladomyrma* species exhibit a strong preference in their patrolling activity on external plant surfaces by concentrating on young foliage and shoots (chapter 8). The concentration of ant activity on intact young, vulnerable plant tissue is a striking phenomenon shared among many plant-ant taxa (e.g., JANZEN 1972, RISCH 1982, FIALA & MASCHWITZ 1990, FONSECA 1994, GAUME & MCKEY 1998, GRANGIER et al. 2008), and I have proposed to call this strong, fundamental behavioural trait '**neophily'**. In all host plants of *Cladomyrma* the production of new leaves is linked to the production of ant housing structures, thus facilitating ant-mediated protection of young leaves against insect herbivores. Other behavioural traits are also of potential benefit to the host plants: *Cladomyrma* workers of established colonies that have reached a certain size strongly react to the disturbance of the plants and show an alarm response when confronted with leaf injuries. These traits, alone or in combination, may select for the development of caulinary domatia.

These three key traits –access to live stems, utilisation of indirect food rewards via trophobionts and 'neophily'– may function as evolutionary routes to new obligate host associations in the *Cladomyrma* system. But how great is the potential for the colonisation of 'wrong' host plants by ant queens?

Although the ability of plant-ant queens to locate and colonise specific hosts, and their absence from others, provide some of the strongest evidence of evolutionary specialisation to symbiosis with particular plants, the potential to associate successfully with a 'wrong' host is probably greater than we often realise (BRONSTEIN, DIECKMANN & FERRIÈRE 2004). For example, many solitary bees visit only one or very few plant species for pollen. When flowering of the usual host fails, many of these bees can shift successfully to plant species with which they are almost never associated under normal conditions (WCISLO & CANE 1996). Native fig wasps have been recorded to visit introduced fig species at a very low, but detectable, frequency (NADEL, FRANK & KNIGHT 1992). With the exception of some extreme specialists, mobile partners within mutualisms, such as plant-ants, *"have the ability to move among alternative partners by making choices of who to visit, who to ignore, who to abandon, and when to abandon them"* (BRONSTEIN, ALARCÓN & GEBER 2006). The flexibility in host-choice by certain plant-ants, including *Cladomyrma petalae*, has already been highlighted in a previous chapter (5).

'Wrong' hosts have been recorded from many ant/plant systems worldwide (DAVIDSON & MCKEY 1993a, FIALA et al. 1999), but these 'mismatches' often produce fitness effects because hosts appear to be of poor quality (*Pachycondyla luteola*/*Cecropia membranacea*: YU & DAVIDSON 1997; *Crematogaster borneensis*/*Macaranga winkleri*: ITINO et al. 2001b; *Pheidole minutula*/*Tococa bullifera*: NERY & VASCONCELOS 2003).

Mostly the 'wrong' host is a myrmecophyte closely related to the 'usual' host species, belonging to the same ant-plant lineage, but occasionally colonisations of non-myrmecophytic species have been observed. Dead founding queens of *Crematogaster* (*Decacrema*) morphospecies 2, usually inhabiting *Macaranga hosei*, were found in saplings of Bornean *M. gigantea* (BRIGITTE FIALA, pers. comm.). Founding queens of two *Azteca* species, *A. constructor* and *A. xanthochroa*, may be found in saplings of *Cecropia polyphlebia*, a non-myrmecophytic cloud-forest plant, but mature trees always lack ant colonies. These queens are presumably doomed dispersants from lower elevations (LONGINO 1991a+b). Founding queens of *Myrmelachista flavocotea*, an obligate inhabitant of understorey treelets in the genus *Ocotea*, have been collected in stump sprouts of other Lauraceae that become large canopy trees, but no large trees have ever been found hosting a colony of *M. flavocotea* (LONGINO 2006). The colonisation of these trees by founding queens may result from unavailability of more suitable hosts.

A few scattered observations provide evidence that founding queens of *Cladomyrma* occasionally colonise wrong hosts. Queens of *C. hewitti*, a regular occupant of myrmecophytic *Neonauclea* in Borneo, were twice collected from domatia of a closely related but unspecific ant-plant *Myrmeconauclea strigosa* in Brunei (CARINE BROUAT & DOYLE MCKEY, pers. comm.). At the collection site *Neonauclea* ant-plants grew in close vicinity to *Myrmeconauclea* and they were probably the source of *C. hewitti* queens. A founding queen of *Cladomyrma dianeae*, also a regular occupant of Bornean *Neonauclea*, has probably been collected from an unknown *Fagraea* species (D. DAVIDSON, pers. comm.), but the identification of the host needs to be verified.

In one case we may even witness an initial stage of a host expansion process by *Cladomyrma*. Several features of the association between *Cladomyrma petalae* and the climber *Strychnos vanprukii* differ sharply from other ant/plant relationships in the system: i) ant occupancy is apparently restricted to a few populations in the Malay Peninsula, ii) both ant colony size on a given plant and occupancy rate within a population is exceptionally low, and iii) alate sexuals in *Strychnos* have not been found (see page 75). This 'weak' relationship between ant and plant suggests a host expansion in progress or, alternatively, it is an old association in which, for some reason, the further specialisation is impeded.

Despite this admittedly anectodal evidence that host expansion and 'erroneous' host colonisations presently occur in the *Cladomyrma* system, it cannot be disputed that such events must have happened in the past which led to the current broad host plant range of the genus. Many adult insects demonstrate a preference for the host species on which they themselves developed and mechanisms such as early learning, imprinting, imaginal conditioning, familiarisation is known to facilitate host-choice and host fidelity in arthropods (GARCIA-PÉREZ 1987, DEJEAN 1990, DJIETO-LORDON & DEJEAN 1999, BARRON 2001, EGAS & SABELIS 2001). Although the mechanisms of host-choice in plant-ants are not well understood (see chapter 5) I speculate that experience of female alates on new hosts could play a role in the maintenance of a newly acquired host in *Cladomyrma*. An accidental shift from one host plant species to another could even result in the formation of host races (WOOD et al. 1999) or isolation between parental and derived populations, eventually resulting in new species (PRICE 2002).

To sum up, I suggest that three **key traits** of *Cladomyrma* favour niche differentiation and the acquisition of new hosts over evolutionary time.

1) The ability of queen ants to hollow out live stems for colony foundation facilitates access of hosts possessing no myrmecophytic specialisations.

2) *Cladomyrma* acquires and maintains association with polyphagous trophobionts and hence can thrive in plants that provide no direct, specialised food reward.

3) 'Neophily' and other behavioural traits of *Cladomyrma* provide a potential benefit for the host plant. This, in turn, imposes constraints on the host that may select for the development of caulinary domatia.

Taken together, I hypothesise that these three key traits have resulted in *Cladomyrma* conserving the potential to colonise new hosts and creating unique niches.

12. Summary

In over 100 genera of tropical angiosperms, one or more species possess specialised structures for housing ants. The longevity and intimacy of these associations has often facilitated an increasing specialisation of both the ants and the plants, leading to a number of highly specific and obligate symbioses. However, the number of known ant-plants and its associated ants in south-east Asia remained on a low level compared to the Neotropics. Early literature contained only few anecdotal reports of the ant genus *Cladomyrma* WHEELER inhabiting (unidentified) plants. This work presents the new findings on *Cladomyrma* and its host plants that accumulated over the last two decades. My studies of *Cladomyrma* reveal that there is a largely overlooked community of south-east Asian plant-ants and their associated plants. In spite of being species-rich and abundant this lineage of ants had been almost never collected.

In cooperation with DONAT AGOSTI the new species collected receive a formal taxonomic treatment. Currently the genus consists of at least 12 species. *Cladomyrma* has been thought to be restricted to the ever-wet part of the West Malesian floristic region, comprising the Malay Peninsula, Borneo, and Sumatra, but recent collections from Thailand and Vietnam indicate that species of the genus penetrate the seasonal tropical forests of Continental Asia.

Cladomyrma inhabits 24 plant species belonging to a surprisingly extensive range of plant taxa: *Callerya*, *Saraca*, *Spatholobus* (Fabaceae), *Crypteronia* (Crypteroniaceae), *Drypetes* (Putranjivaceae), *Ryparosa* (Achariaceae), *Strychnos* (Loganiaceae), *Neonauclea* (Rubiaceae), *Luvunga* (Rutaceae) and *Sphenodesme* (Lamiaceae). These 10 host plant genera from eight plant families comprise about 50% of all non-epiphytic plant genera, which are known to be regularly associated with specialised stem-nesting ant partners in the Oriental region. In terms of taxonomic diversity on the genus and family level the range of hosts utilised by *Cladomyrma* is one of the broadest ever recorded for any live stem-nesting plant-ant lineage worldwide.

This work provides a species-level overview of all *Cladomyrma* host plants known from Borneo, the Malay Peninsula and Sumatra, including descriptions of ant-housing structures (domatia), ant inhabitant identity, onset of colonisation during plant ontogeny, nest structure, occupancy rate, and considerations of results obtained from herbarium specimens. Both the regularity of ant association and the degree of morphological specialisation toward myrmecophytism are assessed.

The behavioural traits of *Cladomyrma* are compatible with traits exhibited by other protective plant-ants. This work demonstrates that all species of *Cladomyrma* investigated (*dianeae*, *maschwitzi*, *yongi*, *petalae*) confer antiherbivore protection to young leaves of its host. The ants also attack and repell or kill herbivorous insect larvae encountered on young foliage. Cleaning behaviour appears to be a trait shared by all members of the genus, and the two species tested (*maschwitzi*, *petalae*) successfully removed termite eggs experimentally placed onto young leaves. Another trait common to all known species of the genus is that the ants preferentially patrol young shoots and leaves ('neophily'). These behavioural traits of *Cladomyrma* likely reduce stem damage and pathogenic infection of their host. The ants prune encroaching vegetation (tested in *dianeae maschwitzi*, *petalae*, *yongi*, observed in *crypteroniae*) and attack paper tape used to mark host plants (observed in *andrei*, *dianeae*, *hobbyi*, *nudidorsalis*, *maschwitzi*, *yongi*, *petalae*). If these traits combined translate into a better reproductive success of the hosts has yet to be verified. Evidence for lifetime fitness benefits is particularly difficult to quantify for the long-lived woody host plants of *Cladomyrma*.

The predominant food source of *Cladomyrma* appears to be the honeydew of scale insects (Coccidae and Pseudococcidae) which the ants tend inside their nest cavities. Observations on scale insect acquisition by *Cladomyrma* foundress queens show that hemipteran trophobionts are not transported by the queens on their nuptial flight but they nevertheless arrive on the host plant independently of the ants. Entry into nest chambers is facilitated by small holes kept open by the foundress queen.

Most *Cladomyrma* species have been recorded from only one or two (three) host plant species (*andrei*, *crypteroniae*, *hobbyi*, *maschwitzi*, *nudidorsalis*, *scopulosa*, *yongi*), but two species, *Cladomyrma petalae* and *C. dianeae*, are more catholic in their host usage; the first being a 'generalist' plant-ant colonising hosts across a broad taxonomic range, the second inhabiting several members of the genus *Neonauclea*. First results of host-choice experiments with *C. petalae* are presented and the potential mechanisms promoting host specificity are discussed.

My studies of the *Cladomyrma*/plant associations indicate that codiversification and host shifts or host expansions, rather than cospeciation, shape the pattern of species interactions in this system. Finally, I propose a scenario in which three key traits of *Cladomyrma* –access to live stems, utilisation of indirect food rewards via trophobionts and 'neophily'– are hypothesised to favour niche differentiation and the acquisition of new hosts over evolutionary time.

13. Ausführliche Zusammenfassung

13.1. Einleitung

Die Pflanzen der tropischen Regenwälder können einem persönlichen Kontakt mit Ameisen nicht ausweichen. Letztere sind in diesen Lebensräumen allgegenwärtig und stellen einen großen Teil der tierischen Biomasse und Individuenzahl. Was geschieht, wenn diese zwei Welten aufeinander treffen?

Der Gegenstand der hier vorliegenden Dissertation ist eine bisher fast unbekannte Ameisen-Pflanzen-Symbiose in Südostasien. Die Ameisen der Gattung *Cladomyrma* gehen Assoziationen mit einer ungewöhnlich großen Zahl an Wirtspflanzen ein. Diese Arbeit schlägt einen weiten Bogen und untersucht verschiedene Aspekte der Verhaltensökologie von *Cladomyrma*, zum Beispiel die Koloniegründung in einer Wirtspflanze, die Wirtswahl durch die Ameisenkönigin, die Aufnahme von trophobiotischen Läusen in die Kolonie und den Schutz des Wirtes gegen herbivore Insekten. Einen großen Raum nimmt die Untersuchung der Wirtspflanzen ein: a) in welcher Phase ihrer ontogenetischen Entwicklung werden sie besiedelt, b) weisen die ameisenbeherbergenden Strukturen Anpassungen an die Ameisenbesiedlung auf, und c) wie hoch sind die Besiedlungsraten. Ergänzt werden diese Ergebnisse durch die Sichtung umfangreichen Herbarmaterials. Ein weiterer Teil dieser Studie untersucht die Taxonomie von *Cladomyrma* und das Wirtsspektrum der jeweiligen Arten, um den Grad der Wirstspezifität einschätzen zu können.

Diese Aspekte berühren einige fundamentale biologische Fragestellungen wie die Koexistenz von Arten, die Schutzsysteme von Pflanzen gegen Herbivoren oder die Evolution von interspezifischen Mutualismen. Welche Faktoren fördern die enge Interaktion zwischen unverwandten Organismen? Spielen koevolutive Prozesse in Ameisen-Pflanzen-Assoziationen eine Rolle?

Arten in über hundert Gattungen tropischer Angiospermen besitzen spezialisierte Strukturen zur Beherbergung von Ameisen. Diese ‚Ameisenwohnungen' bilden eine wichtige Voraussetzung für konstante und langlebige Assoziationen zwischen Pflanze und Ameise, und führen nicht selten zu hochspezifischen und obligaten Symbiosen. Es wurde die Hypothese aufgestellt, daß Ameisen, die ihre Wirtspflanze besser beschützen, und Pflanzen, die mehr in den Erhalt ihrer Partnerameisen investieren, damit das eigene Überleben und ihren Reproduktionserfolg verbessern. Sind die Gemeinschaften, die *Cladomyrma* mit Wirtspflanzen eingeht, solche ‚wahren' Mutualismen?

13.2. Revision der Gattung *Cladomyrma*

Die Arten der Ameisengattung *Cladomyrma* blieben lange unbekannt. Fast hundert Jahre nach der Erstbeschreibung im Jahre 1894 waren erst drei *Cladomyrma*-Arten wissenschaftlich bekannt, ihre Lebensweise blieb weiterhin ein Rätsel. Erst die Wiederentdeckung von *Cladomyrma* durch ULRICH MASCHWITZ vor zwei Jahrzehnten warf neues Licht auf eine kryptisch lebende, aber in Südostasien weit verbreitete Ameisengattung. Die in Zusammenarbeit mit DONAT AGOSTI anhand morphologischer Merkmale erstellte Revision der Gattung erkennt nun 11 Arten an, eine weitere Art wurde kürzlich aus Vietnam beschrieben. Jüngere Funde aus Thailand stellen möglicherweise neue Arten dar, eine taxonomische Beschreibung steht aber noch aus (SEIKI YAMANE, pers. Mitteilung). Es ist zu erwarten, daß weitere Aufsammlungen, insbesondere aus schwer zugänglichen Gebieten im Inneren Borneos, die Artenzahl noch weiter erhöhen werden. Zur Zeit umfaßt die Gattung mindestens 12 Arten, von denen allein neun –sieben davon endemisch– in Borneo vorkommen. Das Verbreitungsgebiet der meisten Arten ist beschränkt, mit Ausnahme von *Cladomyrma crypteroniae* und *C. maschwitzi*. Letztere weist die größte bekannte Verbreitung auf, gefunden wurde die Art sowohl in Borneo und Sumatra als auch auf der Malaiischen Halbinsel.

13.3. Das Wirtspflanzenspektrum

Vor etwa zwei Jahrzehnten wurden die ersten drei Wirtspflanzen-Arten von *Cladomyrma* identifiziert. Seitdem konnte durch diese Untersuchung die Anzahl der bekannten Wirtsarten deutlich erhöht werden. Extensive Feld- und Herbariumstudien haben nun ein Wirtsspektrum aufgedeckt, das 24 Arten aus 10 verschiedenen Gattungen und acht Familien umfaßt: *Callerya*, *Saraca*, *Spatholobus* (Fabaceae), *Crypteronia* (Crypteroniaceae), *Drypetes* (Putranjivaceae), *Ryparosa* (Achariaceae), *Strychnos* (Loganiaceae), *Neonauclea* (Rubiaceae), *Luvunga* (Rutaceae) und *Sphenodesme* (Lamiaceae).

Der größte Teil der Wirtstaxa wird regulär und primär nur von *Cladomyrma* besiedelt, Arten aus anderen Ameisengattungen spielen in manchen Fällen eine Rolle als Sekundärbesiedler. Ameisenpflanzen aus der Gattung *Neonauclea* bilden hier eine Ausnahme, da mehrere Arten, die außerhalb des Verbreitungsgebiets von *Cladomyrma* auftreten, von spezialisierten *Crematogaster*-Ameisen besiedelt werden. *Neonauclea* ist auch die einzige Wirtsgattung, in der eine nennenswerte Radiation an Ameisenpflanzen stattgefunden hat (insgesamt 17, von denen alle acht borneensischen Arten mit *Cladomyrma* assoziiert sind). Hinsichtlich der taxonomischen Diversität auf Gattungs- und Familienniveau ist das von *Cladomyrma* genutzte Wirtsspektrum eines der größten weltweit, welches jemals für eine Lineage von

Pflanzenameisen verzeichnet wurde. In der Orientalischen Faunenregion stellen die Wirtspflanzen von *Cladomyrma* etwa 50% aller nicht-epiphytischen Gattungen, die regulär von in lebenden Stämmen nistenden Pflanzenameisen besiedelt werden.

13.4. Unterschiede zwischen den Wirtspflanzen

Die Wirtspflanzen zeigen nicht nur eine hohe taxonomische Diversität, sondern unterscheiden sich zum Teil auch deutlich hinsichtlich ihrer Verbreitung, ihres Lebensraums, der Wuchsform und den äußerlich sichtbaren Anpassungen der ameisenbeherbergenden Strukturen.

Bis auf wenige Ausnahmen stimmen die Verbreitungsgebiete von *Cladomyrma* und ihren Wirtspflanzen überein. *Strychnos vanprukii* und *Drypetes longifolia* besitzen eine deutlich größere geographische Verbreitung als ihre Ameisenpartner, aber dies ist möglicherweise nur Folge einer unscharfen Artabgrenzung. Das Herbarmaterial der betreffenden Arten gibt Anlaß zu der Vermutung, daß beide Arten zu weit gefasst sein könnten.

Es werden die unterschiedlichsten Habitate besiedelt, von natürlichen Störungszonen innnerhalb von Primär- und Sekundärwäldern über Kalksteinhabitate und schattigen Unterwuchs bis hin zu stark anthropogen beeinflußten Regionen mit Vertretern früher Sukzessionsvegetation (*Neonauclea gigantea*). Überraschenderweise sind fünf der 24 Wirtspflanzen-Arten als Kletterpflanzen einem Pflanzentyp zuzuordnen, der unter Ameisenpflanzen selten anzutreffen ist (*Callerya nieuwenhuisii*, *Luvunga* sp., *Spatholobus bracteolatus*, *S. oblongifolius* und *Strychnos vanprukii*). Schließt man die Ameisen-Symbiosen von *Camponotus* mit kletternden Rattanpalmen aus, ist *Cladomyrma* weltweit der dominierende Besiedler von Lianen.

Alle *Cladomyrma*-Arten leben ausschließlich in lebenden Stämmen, deren Mark die Ameisen selbst aushöhlen müssen. Natürlich hohle Internodien bietet keine der Wirtspflanzen an (mit einer partiellen Ausnahme), aber in manchen Eigenschaften wie der Zugänglichkeit, Form, Größe oder dem zeitlichen Auftreten in der Wirtspflanzen-ontogenese unterscheiden sich die ameisenbeherbergenden Strukturen zum Teil deutlich. Gruppiert man die ‚Ameisenwohnungen' hinsichtlich ihrer offensichtlichen Anpassung an die Ameisenbesiedlung ergeben sich fünf Gruppen. Diese Unterscheidung muß aber vorerst als provisorisch betrachtet werden, da histologische Studien der Stammanatomie der Wirtspflanzen und ihrer nicht-myrmekophytischen Verwandten nötig sind, um versteckte morphologische Anpassungen, welche zum Beispiel das Aushöhlen oder den Zugang durch Ameisen erleichtern, erkennen zu können.

Die **erste Gruppe** besteht aus nur einer Wirtspflanze, die keinerlei äußerlich erkennbaren Anpassungen des Stammes an Ameisenbesiedlung erkennen läßt. Die Internodien von *Strychnos vanprukii* sind weder in jungen noch in älteren Pflanzen angeschwollen, auch nicht an den Nodien, an denen die Blätter ansetzen. Ein sogenanntes ‚Prostoma', eine den Zugang für Ameisen erleichternde, dünnwandige Stelle, ist an den Internodien nicht vorhanden. Die Pflanze wird frühestens ab einer Länge von etwa 1,5 m besiedelt, da in kleineren Pflanzen der Markkanal nicht den notwendigen Durchmesser erreicht, um Ameisenköniginnen von *Cladomyrma* aufzunehmen. Die Besiedlungsrate liegt deutlich unter derjenigen anderer Wirtspflanzen-Arten im selben Untersuchungsgebiet. Die Pflanze produziert neben markgefüllten Internodien auch solche, die durch Markdegeneration natürlicherweise hohl werden. Der Anteil hohler Internodien nimmt mit der Pflanzengröße zu. Hohle Zweigabschnitte sind zwischen den soliden scheinbar zufällig verteilt, ein Verteilungsmuster war nicht erkennbar. *Cladomyrma*-Königinnen scheinen allerdings nicht zwischen hohlen und soliden Internodien zu unterscheiden.

Die **zweite Gruppe** besteht aus Wirtspflanzen, deren Internodien ebenfalls keine Anschwellungen aufweisen. Ihre Nodien sind allerdings leicht bis stark verdickt, möglichweise, um die vaskuläre Versorgung und/oder die mechanische Stützung der großen Blätter zu gewährleisten (*Crypteronia*, *Ryparosa*, *Saraca*). Damit verbunden ist eine deutliche Größenzunahme des Markkanals im Bereich des Nodiums. Durch Aushöhlen dieses Stammbereiches werden Koloniegründungen in jungen Pflanzen möglich, deren primärer Internodiendurchmesser für Ameisenköniginnen noch nicht ausreichend ist. Besiedlung durch *Cladomyrma* setzt in Pflanzen ab einer Höhe von etwa 0,4–0,8 m (*Crypteronia*, *Ryparosa*) oder ab 1,0 m ein (*Saraca*). Prostomata scheinen nicht entwickelt zu sein. Besiedlungsraten sind hoch, aber die Assoziation mit *Cladomyrma* geht in großen, reproduktiven Bäume von *Crypteronia* und *Saraca* verloren.

Die Kletterpflanze *Luvunga* sp. verweist schon auf die dritte Gruppe und scheint eine Zwischenstellung einzunehmen. Die Pflanze geht erst ab etwa 2 m Höhe zu einer kletternden Lebensweise über, vorher erscheinen Jungpflanzen als kleine Bäumchen. Der Stamm älterer Pflanzen weist offensichtlich keine geschwollenen Internodien oder verdickten Nodien auf, allerdings zeigen Jungpflanzen leicht aufgeblähte Internodien, deren Durchmesser zum Nodium hin ansteigt. In diesen Bereichen erscheint das Mark locker und weich. Bereits die Internodien von Jungpflanzen nicht größer als 0,2–0,5 m können groß genug sein, um von Ameisenköniginnen als Gründungskammern ausgehöhlt und genutzt werden zu können.

Die **dritte Gruppe** wird charakerisiert durch Wirtspflanzen, deren junge Stämme oder Zweige regelmäßig geschwollene Abschnitte aufweisen (*Drypetes*). Diese hypertrophen Domatien erstrecken sich normalerweise über ein bis zwei(einhalb) Internodien. Das Mark ist heterogen, in den aufgeblähten Abschnitten ist es weiß, weich und besitzt großvolumige Zellen, während die unmodifizierten Abschnitte ein vergleichsweise hartes, kompaktes Mark aufweisen. In Jungpflanzen besiedeln *Cladomyrma*-Kolonien nur die geschwollenen Stammabschnitte, dagegen werden in älteren Pflanzen mit einem größeren Primärdurchmesser der Zweige auch die ungeschwollenen Abschnitte ausgehöhlt und als Nestraum genutzt. Besiedlungsraten sind hoch.

Die **vierte** Gruppe ähnelt der dritten, doch besteht sie ausschließlich aus Lianen (*Callerya*, *Spatholobus*). Dies hat Konsequenzen für die Ausprägung der Domatien in Jungpflanzen. Letztere besitzen einen im Vergleich zu Bäumen ausgesprochen geringen Primärdurchmesser mit entsprechend kleinem Markkanal. Eine frühe Besiedlung durch Ameisenköniginnen wird hier durch die Ausbildung von stark hypertrophierten Domatien mit weichem Mark ermöglicht. Wie zuvor werden in älteren Pflanzen auch die unmodifizierten Stammabschnitte besiedelt, da deren Markkanal nun ausreichend groß ist.

Die **fünfte Gruppe** besteht aus den *Neonauclea*-Arten. Sie alle entwickeln verdickte Domatien, die immer in ähnlicher Weise am gleichen Ort ausgebildet werden. Das basale Internodium jedes neuen Seitentriebes entwickelt im distalen Abschnitt eine Anschwellung, die sich über ein bis zwei Drittel des gesamten Internodiums erstreckt. Die relative und absolute Länge der Domatien variiert sowohl innerhalb als auch zwischen den Arten. Der tragende Stamm, die Hauptachse, bildet im Gegensatz zu allen anderen Wirtspflanzen keine Domatien aus und bleibt durchweg unbesiedelt. Jedes Domatium weist lateral auf beiden Seiten ein Prostoma auf, einen dünnwandigen Bereich, der sich als schmales Band über die ganze Domatienlänge zieht. Nur hier beißen *Cladomyrma*-Ameisen ihre Eingänge. Das Mark ist im Domatienbereich deutlich weicher, es wird aber nicht vollständig abgebaut wie in anderen myrmekophytischen *Neonauclea*-Arten, die außerhalb Borneos von spezialisierten *Crematogaster*-Ameisen besiedelt werden.

Die Unterschiede der Wirtspflanzen hinsichtlich ihrer ameisenbehergenden Strukturen (erstes Auftreten, Stammdurchmesser, Mark, Prostoma) werden ausführlich diskutiert und als mögliche Präadaptation bzw. als Merkmale einer Spezialisierung an die Ameisenbesiedlung gedeutet. Unzweifelhaft ist, daß Myrmekophytie in diesem System viele Male entstanden sein muß.

13.5. Nutzen der *Cladomyrma*-Besiedlung für die Wirtspflanzen

Es konnte gezeigt werden, daß alle untersuchten *Cladomyrma*-Arten (*dianeae*, *maschwitzi*, *yongi*, *petalae*) den Fraßschaden an jungen Blättern ihrer Wirte signifikant reduzieren. Die Ameisen attackieren Insekten, insbesondere deren Larven, bis diese getötet oder vertrieben sind. ‚Säuberungsverhalten' scheint allen *Cladomyrma*-Arten gemein zu sein, und die zwei getesteten Arten (*maschwitzi*, *petalae*) entfernten erfolgreich die experimentell auf jungen Blättern plazierten Termiteneier. Ein weiteres auffälliges Merkmal, das bei allen Arten auftritt, ist die Präferenz der Arbeiterinnen in ihrer Außenaktivität für junge, sich entwickelnde Pflanzenteile. Die potentiellen proximaten sowie ultimaten Gründe für diese ‚Neophilie' werden ausführlich diskutiert. Diese Beobachtungen stützen die ‚Optimal Defense Hypothesis', die von der Annahme ausgeht, daß Antiherbivorschutz auf die wertvollsten und verletzlichsten Pflanzenteile konzentriert sein sollte.

Cladomyrma attackiert und stutzt die auf die Wirtspflanze übergreifende Vegetation (getestet mit *dianeae maschwitzi*, *petalae*, *yongi*, beobachtet in *crypteroniae*) und zerstört Klebeband, welches zur Markierung von Wirtspflanzen verwendet wurde (beobachtet in *andrei*, *dianeae*, *hobbyi*, *nudidorsalis*, *maschwitzi*, *yongi*, *petalae*). Dennoch ist der Nutzen des ‚Rankenbeißens' –z.B. die Entfernung von um Licht konkurrierende Pflanzen– für die Wirte alles andere als klar. Die Reaktion der Ameisen auf experimentell an die Wirte angebrachte Fremdtriebe war für die untersuchten Arten variabel und manchmal recht ineffektiv. Möglicherweise spielt in diesen Fällen noch eine andere Funktion eine Rolle, nämlich die Minimierung der Zugangsmöglichkeiten für konkurrierende Ameisen auf die Wirtspflanze.

Es gibt keinen Hinweis darauf, daß die Wirtspflanzen einen mehr als vernachlässigbaren Teil ihrer Nährstoffe (z.B. Stickstoff und Phosphor) über den Abfall oder die Fäzes der sie besiedelnden Ameisenkolonie erhalten.

Insgesamt kann man sagen, daß ein kurzfristiger Schutzeffekt wenigstens für einige *Cladomyrma*-Arten unzweifelhaft gegeben ist, und die von *Cladomyrma* gezeigten Verhaltensweisen mit denen anderer Pflanzenameisen übereinstimmen, die ihre Wirte nachweislich schützen. Ob sich dies aber in einem höheren Reproduktionserfolg der Wirtspflanzen niederschlägt, bleibt noch zu klären. Der Nachweis eines Nutzens der Besiedlung mit *Cladomyrma* über die gesamte Lebensdauer ist für die langlebigen Wirtspflanzen nur mit enormem Aufwand experimentell zu ermitteln.

13.6. Kosten der *Cladomyrma*-Besiedlung für die Wirtspflanzen

Der Unterhalt einer *Cladomyrma*-Kolonie ist für die Wirtspflanze mit Kosten verbunden, da die Ameisen indirekt über Schild- und Schmierläuse (Coccidae und Pseudococcidae) die Ressourcen der Pflanze anzapfen. Honigtau scheint die bedeutendste Nahrungsquelle der Kolonie zu sein, aber extrafloraler Nektar kann, wenn verfügbar, z.B. in Hungersituationen genutzt werden.

Die Bedeutung der Läuse-Trophobionten als entscheidende Nahrungsquelle für die Kolonie wird durch mehrere Beobachtungen deutlich. Bereits in einer frühen Phase der Kolonieentwicklung werden die Läuse erworben. Ihr Ausbleiben scheint eine erfolgreiche Koloniegründung zu verhindern. Die koloniegründenden Ameisenköniginnen haben zudem eine spezielle Verhaltensweise entwickelt: durch Anlegen schmaler Schlitze wird den wohl meist windverbreiteten Jungstadien der Läuse der Zugang in die Gründungskammer erleichtert. Zudem sind die Läuse während der gesamten Lebensdauer der Kolonie anwesend, Kolonien ohne Läuse wurden niemals angetroffen. Bei Verletzung des Stammes bringen die Arbeiterinnen nicht nur ihre Larven in Sicherheit sondern sie transportieren auch ihre Läuse in unverletzte Nestbereiche.

Es ist anzunehmen, daß die Pflanze keinen oder nur einen geringen Einfluß auf den über Honigtau vermittelten Nahrungsfluß in Richtung Ameise hat. Allerdings gibt es bisher keinen Hinweis auf eine Übernutzung der Wirtspflanzen durch *Cladomyrma*, denn die Populationsdichte der Läuse scheint durch die Ameisen geregelt zu werden. Möglicherweise nutzen die Ameisen die Läuse auch selbst als Proteinnahrung.

Ameisenpflanzen stellen für einige Prädatoren (Spechte, Nagetiere, Affen) eine reiche und vorhersehbare Quelle an Ameisennahrung dar. Die Schädigung des Wirtes durch aufgebrochene Domatien und Äste kann in manchen Populationen bedeutend sein. In einem monospezifischen, stark gestörten Standort von *Neonauclea gigantea* besaßen über die Hälfte der Bäume (n=226) mindestens ein Domatium, das durch Nagetiere aufgebissen war. Wenn auch weit weniger dramatisch, so sind Schäden durch Myrmekophagie in mehreren Wirtspflanzen von *Cladomyrma* gelegentlich beobachtet worden (*Spatholobus bracteolatus*, *Drypetes longifolia*, *Neonauclea* spp., *Luvunga* sp. und *Crypteronia griffithii*).

Eine ganze Reihe weiterer Kosten kommen für die Wirtspflanze prinzipiell in Frage, so zum Beispiel die Ausbildung von Domatien in Jungpflanzen und die damit verbundene Investition in Stammgewebe. Die potentielle Bedeutung für das *Cladomyrma*-System wird diskutiert.

13.7. Brauchen Wirtspflanzen *Cladomyrma* für ihr Überleben?

Unbesiedelte Wirtspflanzen sind in einigen Fällen beobachtet worden, die Gründe für das Fehlen der Ameisenpartner scheinen jedoch sehr unterschiedlich zu sein. 1) Die Assoziation geht im Verlauf der ontogenetischen Entwicklung verloren (*Crypteronia griffithii*, *Saraca thaipingensis*). 2) Störungen wie Myrmekophagie können lokal für ameisenfreie Pflanzen verantwortlich sein. 3) Windverbreitete Wirte (*Neonauclea*) scheinen sich manchmal außerhalb der Flugdistanz koloniegründender *Cladomyrma*-Königinnen etablieren zu können. 4) Die ökologische Toleranz der Wirtspflanzen übersteigt die der Ameisen; *Neonauclea* tritt vereinzelt in Höhen auf, die oberhalb der Höhengrenze von *Cladomyrma* liegen. 5) Die Assoziation (*Strychnos vanprukii*) steht am Anfang ihrer evolutionären Entwicklung oder, alternativ, Selektionsdrücke wirken auf die Assoziation in verschiedene Richtungen und verhindern so ihre weitere Spezialisierung. 6) Der Baum *Saraca thaipingensis* wird aufgrund seiner Blütenpracht außerhalb des natürlichen Lebensraums als Zierpflanze in Parks genutzt. Hier scheint der Baum auch ohne Ameisenschutz gut zu gedeihen.

Die Besiedlungsraten der Wirtspflanzen von *Cladomyrma* schwanken je nach Wirtsart, Entwicklungsstadium oder Habitat zwischen 35–100%, in den meisten Fällen liegt die Besiedlungsrate aber oberhalb von 80%. Diese Befunde deuten darauf hin, daß die Ameisenbesiedlung für das Überleben vieler Wirtspflanzen keine Frage des Alles-oder-Nichts darstellt. In Verbindung mit den offensichtlichen Anpassungen an die Ameisenbesiedlung (Domatien) läßt sich jedoch aus den hohen Besiedlungsraten einiger Wirtspflanzen mit hoher Wahrscheinichkeit ableiten, daß mit der erfolgreichen Etablierung einer *Cladomyrma*-Kolonie ein erhöhter Reproduktionserfolg der Pflanzen verbunden ist.

13.8. Nutzen und Kosten aus Sicht der Ameisen

Die Vorteile der Besiedlung einer myrmekophytischen Pflanze liegen für *Cladomyrma* auf der Hand: Wohnraum und Nahrungsquelle sind in einem langlebigen, geschützten Nistplatz vereint. Des weiteren bieten viele Wirte von *Cladomyrma* bereits als Jungpflanzen Domatien an, so daß eine frühe Besiedlung und Monopolisierung des Wirtes durch eine Kolonie ermöglicht wird. Beides ist geeignet, die interspezifische Konkurrenz von Ameisen um Nistplätze deutlich zu reduzieren. Zudem sind alle Ameisenaktivitäten auf der Pflanzenoberfläche nie weit von einem Nesteingang entfernt. Rekrutierung von Koloniemitgliedern oder Flucht erfolgen somit über geringe Distanzen.

Durch die enge Verbindung von *Cladomyrma* mit ihrem Wirt entstehen den Ameisen allerdings auch Nachteile, die mit der seßhaften Lebensweise der Pflanze verbunden sind. Werden die Lebensbedingungen ungünstig, ist ein Standortwechsel nicht mehr möglich, denn freie bzw. ‚leere' Wirte in unmittelbarer Nachbarschaft stehen in der Regel nicht zur Verfügung.

Ein weiteres Problem besteht darin, daß sich die Partner unabhängig voneinander verbreiten; die Assoziation wird ‚horizontal' weitergegeben und die Partner müssen sich mit jeder Generation neu zusammenfinden. Dies stellt im hochdiversen Regenwald große Anforderungen an die Fähigkeit der Wirtsfindung von *Cladomyrma*-Königinnen. Die Populationsdichte der Wirtspflanzen ist, je nach Art, Region und/oder Habitat, starken Schwankungen unterworfen, aber selbst Pflanzen in isolierten Vorkommen, zum Beispiel in kleinen Baumsturzlücken oder entlang von Bachläufen, sind in der Regel von *Cladomyrma* besiedelt.

13.9. Wirtsspezifität

Der größte Teil der *Cladomyrma*-Arten ist bisher nur auf ein bis zwei, selten drei Wirtspflanzenarten gefunden worden (*andrei*, *crypteroniae*, *hobbyi*, *maschwitzi*, *nudidorsalis*, *scopulosa*, *yongi*). Zwei Arten zeigen jedoch ein anderes Muster von Wirtsassoziationen. *Cladomyrma petalae* and *C. dianeae* sind hinsichtlich ihrer Wirtsnutzung als promiskuitiv einzustufen, die erste Art besiedelt als ‚generalistische' Pflanzenameise Wirte aus einem breitem taxonomischen Spektrum, die zweite nutzt mehrere Ameisenpflanzen aus der Gattung *Neonauclea*. Erste Ergebnisse von Wirtswahl-Experimenten mit *Cladomyrma petalae* unterstützen die Hypothese, daß trotz der hier wahllos erscheinenden Besiedlung von sechs Wirtsarten aus fünf Pflanzenfamilien die Wirtswahl durch koloniegründende Königinnen nicht zufällig erfolgt. Die möglichen Faktoren, welche die Wirtswahl beeinflussen, werden diskutiert.

13.10. Evolution des Wirtsspektrums

Die Fähigkeit der Ameisenköniginnen ihre spezifischen Wirte zu lokalisieren und zu besiedeln, gilt –in Verbindung mit ihrer Abwesenheit von anderen Pflanzen– als eine der überzeugendsten Belege für die evolutionäre Spezialisierung einer Symbiose mit bestimmten Wirtspflanzen. Dennoch ist das Wirtsspektrum von *Cladomyrma* ungewöhnlich breit und umfaßt eine große Zahl an unverwandten Wirtspflanzen. Myrmekophytie muß daher in diesem System mehrmals unabhängig voneinander entstanden sein. Dies wirft die Frage auf, welche Merkmale als evolutionäre Pfade zur Bildung myrmekophytischer Assoziationen dienen können.

Ich stelle die Hypothese auf, daß drei Merkmale entscheidend dazu beitragen, daß *Cladomyrma* die Fähigkeit bewahrt hat, neue Wirtspflanzen zu besiedeln und –über einen evolutionären Zeitraum– neue, einzigartige Nischen zu schaffen.

1) Koloniegründende Königinnen besitzen die Fähigkeit, lebende Stengel auszuhöhlen. Dies ermöglicht den Zugang zu Wirtspflanzen ohne vorherige myrmekophytische Spezialisierung. 2) *Cladomyrma* unterhält Assoziationen mit dreißig oder mehr Arten von Schmier- und Schildläusen, die zum Teil extrem polyphag sind. *Cladomyrma* kann daher auf Pflanzen gedeihen, die keine spezialisierte Nahrung in Form von Futterkörperchen oder extrafloralem Nektar anbieten. 3) Die Präferenz in der Außenaktivität für junge Pflanzenteile (‚Neophilie') und weitere Verhaltensweisen von *Cladomyrma* sind geeignet, dem Wirt einen potentiellen Nutzen zu bringen. Dies wiederum könnte einen Selektionsdruck auf die Entwicklung von Domatien ausüben.

Diese drei Schlüsselmerkmale –Zugang zu lebenden Pflanzenstengeln, indirekte Nutzung von Pflanzennahrung via Trophobionten und Neophilie– sind mögliche evolutionäre Pfade für die Bildung neuer Assoziationen im *Cladomyrma*-System und erklären das breite Wirtsspektrum aus nicht verwandten Pflanzentaxa.

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15. Appendix

15.1. Table index

15.2. Figure index

15.3. Deposit of *Cladomyrma* specimens in Malaysia

FRIM – Forest Research Institute Malaysia, Kepong, Selangor
SEP – Sepilok, Sabah, Borneo

Cladomyrma andrei

#95-011: several workers (as *C. cryptata*), ex *Calleray nieuwenhuisii*; Poring Hot Springs, Sabah, Malaysia, Borneo; 18.i.1995, Joachim Moog; **SEP**

#95-017: 15 workers, ex *Drypetes longifolia*; Poring Hot Springs, Sabah, Malaysia, Borneo; 26.i.1995, Joachim Moog; **SEP**

Cladomyrma aurochaetae

#97-082: **PARATYPE**; 3 workers, ex *Neonauclea gigantea*; Hose Mountains, Sarawak, Malaysia, Borneo; 03.ii.1997, Joachim Moog; **FRIM**

#97-088: 1 female, ex *Neonauclea* sp.; Hose Mountains, Sarawak, Malaysia, Borneo; 03.ii.1997, Joachim Moog; **FRIM**

Cladomyrma crypteroniae

#97-078: **PARATYPE**; 1 female, ex *Crypteronia griffithii*; Lambir Hills, Sarawak, Malaysia, Borneo; 31.i.1997, Joachim Moog; **FRIM**

#95-090: **PARATYPE**; 3 workers, ex *Crypteronia griffithii*; Lambir Hills, Sarawak, Malaysia, Borneo; 25.ii.1995, Joachim Moog; **FRIM**

Cladomyrma dianae

#91-030: **PARATYPE**; 3 workers, ex *Neonauclea* sp.; Danum Valley, Sabah, Malaysia, Borneo; 06.vii.1991, D. Davidson; **FRIM**

#91-032: 3 workers, ex *Neonauclea* sp.; Danum Valley, Sabah, Malaysia, Borneo; 08.vii.1991, D. Davidson; **FRIM**

#91-012: **PARATYPE**; 1 female, ex *Neonauclea* sp.; Danum Valley, Sabah, Malaysia, Borneo; 29.vi.1991, D. Davidson; **FRIM**

Cladomyrma hewitti

#95-027: 1 alate female, ex *Neonauclea longipedunculata*; km 60.5, Ranau-Telupid road, Sabah, Malaysia, Borneo; 27.i.1995, Joachim Moog; **SEP**

#95-047: 3 workers, ex *Neonauclea* sp.; Crocker Range, Sabah, Malaysia, Borneo; 01.ii.1995, Joachim Moog; **FRIM**

#95-050: 1 female, ex *Neonauclea* sp.; Crocker Range, Sabah, Malaysia, Borneo; 01.ii.1995, Joachim Moog; **FRIM**

Cladomyrma hobbyi

#92-216: 3 workers, ex *Spatholobus oblongifolius*; Lambir Hills, Sarawak, Malaysia, Borneo; 25.ii.1992, Ulrich Maschwitz; **FRIM**

#92-221; 3 workers, ex *Spatholobus oblongifolius*; Lambir Hills, Sarawak, Malaysia, Borneo; 25.ii.1992, Ulrich Maschwitz; **FRIM**

Cladomyrma maryatiae

#93-045: 3 workers, ex *Neonauclea* sp.; Poring Hot Springs, Sabah, Malaysia, Borneo; 14.i.1993, Joachim Moog; **FRIM**

#95-015: 1 female, ex *Neonauclea gigantea*; Poring Hot Springs, Sabah, Malaysia, Borneo; 25.i.1995, Joachim Moog; **FRIM**

#91-031: **PARATYPE**; 1 female and 2 workers, ex *Neonauclea* sp.; Danum Valley, Sabah, Malaysia, Borneo; 08.vii.1991, D. Davidson; **FRIM**

Cladomyrma nudidorsalis

#94-070: **PARATYPE**; 1 female and 2 workers, ex *Drypetes longifolia*; Fraser's Hill, Peninsular Malaysia; 21.ii.1994, Joachim Moog; **FRIM**

Cladomyrma petalae

#91-035: 3 workers, ex *Saraca thaipingensis*; Ulu Gombak, Peninsular Malaysia; 00.ii.1991, Joachim Moog; **FRIM**

#93-143(?): 4 workers, ex *Spatholobus bracteolatus*; Fraser's Hill, Peninsular Malaysia; 24.iii.1993, Joachim Moog; **FRIM**

Cladomyrma yongi

#92-240: **PARATYPE**; 3 workers, ex *Drypetes longifolia*; Lambir Hills, Sarawak, Malaysia, Borneo; 26.ii.1992, Brigitte Fiala; **FRIM**

#92-238: 3 workers, ex *Drypetes longifolia*; Lambir Hills, Sarawak, Malaysia, Borneo; 29.ii.1992, Ulrich Maschwitz; **FRIM**

Cladomyrma sp.

#95-032: 1 female, ex *Neonauclea gigantea*; Road Kota Kinabalu to Tambunan, Sabah, Malaysia, Borneo; 01.ii.1995, Joachim Moog; **SEP**

15.4. AntWeb field guide to *Cladomyrma* (www.antweb.org)

(*C. aurochaetae* is not included)

Cladomyrma andrei

Cladomyrma crypteroniae

Cladomyrma dianeae

Cladomyrma hewitti

Cladomyrma hobbyi

Cladomyrma maryatiae

Cladomyrma maschwitzi

Cladomyrma nudidorsalis

Cladomyrma petalae

Cladomyrma yongi

16. Acknowledgements

A great many people have helped in several ways in the completion of this dissertation.

My first thanks go out to my academic and thesis advisor Prof. Dr. ULRICH MASCHWITZ, to whom I am extremely grateful for inviting me to join his research group and to entrust the subject of this dissertation to my care. Even though my progress in research was interrupted several times, he never ceased to inspire me with new discoveries of ant-plant species and new research ideas. His words of support voiced over the years are greatly appreciated.

Special thanks go to MARIANNE GENSICKE who helped me stay focused on my work. My friend Dr. MARTIN DILL and my cousin EVA HARRISON magnanimously helped in the burdensome task of proof-reading. I am also forever indebted to my brother NORBERT for his support during the final stage of writing up this dissertation.

My field work was done in Malaysia (Malay Peninsula and Borneo). I am thus most indebted to various persons and institutions for the permission to conduct research in Malaysia and to use the facilities of several field stations. I acknowledge with appreciation the help of the supervisors, Dr. AZARAE HAJI IDRIS and Dr. ROSLI BIN HASHIM, of the Ulu Gombak Field Studies Centre, Universiti Malaya, Peninsular Malaysia. The many kindnesses shown me by the staff of the field station, especially Mister BAH TERA, are noted here with gratitude. I wish to thank Datuk LAMRI ALI ALISAPUTRA, director of Sabah Parks, and the Forest Department Kuching for giving me the opportunity to work in Poring Hot Springs, Sabah, and Lambir NP, Sarawak, respectively. Prof. K. E. LINSENMAIR and Dr. BRIGITTE FIALA, Würzburg, provided both accommodation and logistic support at Poring Hot Springs. Also, Dr. FIALA kindly turned over ant specimens from several remote areas in Kalimantan for my use.

I am very grateful for the excellent co-operation with the Forest Research Institute Malaysia (FRIM). Its former director Datuk Dr. SALLEH MOHD NOR gave generous permission to use FRIM facilities and to visit the Pasoh Forest Reserve. Dr. SAW LENG GUAN, head of the FRIM herbarium, has been of invaluable help. My research on host plant taxa would not have been possible without his continuous support. Special thanks are due to Dr. K. MAT-SALLEH and the late K. M. KOCHUMMEN who generously shared their expertise on plant identification. I am indebted to Prof. Dr. WONG KHOON MENG, then curator of the Sandakan herbarium, for permitting me to spend so many days in the herbarium. His enthusiasm and interest in my study is greatly acknowledged.

I owe much to Prof. Dr. PIETER BAAS, then director of the Nationaal Herbarium Nederland (Leiden Rijksherbarium), and his colleagues, especially Dr. JEANNETTE RIDDER-NUMAN. I deeply value the kind and hospitable atmosphere I experienced during my several visits to the Rijksherbarium. The working conditions in Leiden are excellent and the collection of Malesian plants is marvellous. My work on host plant taxa also benefited greatly by visits to the Kew Herbarium, England, and the Philippine National Herbarium, Manila. I thank the curators for granting access to the herbarium collections.

Ms. ANNABEL I. CONSUELO, research officer, kindly helped me in my search for ant-plants at St. Paul's NP, Palawan Island. I am also grateful to Prof. Dr. WEBBER BOOTH, Universiti Brunei Darussalam, both for his hospitality and for giving me the opportunity to visit the Kuala Belalong Field Studies Centre. Special thanks are due to Dr. W. KILLMANN, then chief of the GTZ, Kepong, Malaysia, who provided logistic support.

I am most indebted to Dr. DONAT AGOSTI, American Museum of Natural History, who generously shared his expertise and time to taxonomically describe in co-operation the new *Cladomyrma* ant species that were collected over the years. Dr. DOUGLAS WILLIAMS, British Museum of Natural History, and Dr. PENNY GULLAN, University of California, kindly identified many of the coccoid taxa which live in association with *Cladomyrma* ants. Dr. PETER SEUFERT, then of Würzburg University, helped in identifying lepidopteran species feeding on certain *Cladomyrma* host plants. Dr. MATTHIAS SCHÖLLER provided identifications of herbivorous beetles. I thank them all. The discussions with Prof. Dr. DOYLE MCKEY, CEFE, Montpellier, and Dr. BRUCE WEBBER, CSIRO, Australia, have been a frequent source of inspiration.

Many thanks go out to all my friends and colleagues. It is beyond the scope of these acknowledgements to name all individuals who have facilitated and otherwise made possible my ant-plant studies. Therefore, let it suffice to mention by name just a few whose companionship made my stays in the tropics so memorable and who kindly distracted a considerable part of the mosquito and leech populations: Dr. MARTIN DILL, Dr. WALTER FEDERLE, HARALD GRUNSKY, Dr. HANS-PETER HECKROTH, Dr. CAROLINE LIEFKE, MARLIS MERBACH, GABRIELE RIEDEL, Dr. ANGELA SCHELLERICH, CLAUDIA SEIDEL, Dr. HELMUT STEINER, Dr. ANDREAS WEISSFLOG, and MICHAEL WERNER. I also wish to honour THOMAS DRUDE'S memory, whose untimely death is a deep loss. Special thanks are due to MONICA SCHMIDT both for her tireless help in collecting data on folivory and for her friendship.

My field and herbaria studies on *Cladomyrma* ant-plants would not have been possible without the financial support provided by the DAAD and DFG (Ma 373/17-3, Ma 373/17-4).

17. Publications

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Poster

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Refereeing

Journals
American Journal of Botany
Asian Myrmecology
Biological Journal of the Linnean Society
Compte-Rendus de l'Acadèmie des Sciences, Paris
Insectes Sociaux
Journal of Chemical Ecology
Journal of Insect Science
Journal of Tropical Ecology
Naturwissenschaften
New Phytologist
Oecologia
Selbyana
Zoology

Book
Pasoh: ecology of a lowland rain forest in southeast Asia. Springer Press, Tokyo

Editorial Board

Asian Myrmecology

18. Lebenslauf

19. Erklärung

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Arbeit selbständig angefertigt und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe.

Ich habe diese Dissertation weder in gleicher noch in ähnlicher Form in einem anderen Prüfungsverfahren vorgelegt.

Frankfurt am Main, August 2009